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FURTHER STUDIES ON THE BRAIN OF LIMULUS POLYPHEMUS, WITH NOTES ON ITS EMBRYOLOGY.

W. P. HAY COLLECTION

A number of these horizontal sections proved useful, as when the animal is young, of the length indicated, the bilateral symmetry of the lobes and ganglion cell masses is more marked than in fully grown specimens.

But my main reliance has been some excellent sections made for me three years ago by Dr. H. C. Bumpus. These were transverse, longitudinal (sagittal), and horizontal sections of the brain, removed from living individuals, about 8 inches in length, exclusive of the caudal spine. The transverse and sagittal sections were stained with hæmatoxylin, the horizontal with carmine. I have also made horizontal sections of the brain of the young Limulus, and especially horizontal, sagittal, and transverse sections of the embryos and larvæ in different stages of development. I have found the horizontal sections to be by far the most useful and the various carmine stains the most desirable, since with this stain the central fibers of the lobes remain white or unstained, while the chromatic cells composing what I have called the "nucleogenous bodies" are colored deep carmine, and thus contrast with the other parts of the brain.

In order to comprehend the topography of the brain, while my main reliance has been a study of the horizontal sections, I found it useful to draw models of different sections on cardboard and to mount them on a long insect pin. By the use of this simple device I could obtain a tolerably clear idea of the relations between the lateral and median optic lobes and the cerebral lobes, relations by no means so easily understood as those prevailing in the brains of Crustacea and insects.

Also, at the kind suggestion of Dr. Bumpus, I made a wax model of the brain, and for aid in preparing the sheets of beeswax and for other suggestions I am also indebted to Dr. Bumpus. I made a model from the horizontal, sagittal, and transverse sections; but, owing to the difficulty of painting or otherwise marking the exact limits of the different very irregularly shaped lobes on the sheets of wax, I have not had specially good success in locating on the wax the different lobes and roots of the nerves proceeding from them. The portion of the clearly and distinctly stained nucleogenous bodies can, however, readily be indicated, and as concerns the relations of these masses to each other and to the brain in general the wax models have been quite serviceable. Such models would undoubtedly prove useful in dealing with the brains of insects, Crustacea, and Arachnida, as well as Myriopoda.

II. General Anatomy of the Brain of Limulus.

The nervous system of the Limulus was first described and figured by Van der Hoeven in 1838, the subject of his investigation being *Limulus moluccanus* Latreille, represented by two specimens from the Dutch possessions in the East Indian archipelago. That of the American species, *Limulus polyphemus* Latr., has been described and figured by Sir Richard Owen and afterwards more accurately and with many details by M. A. Milne-Edwards.* It is noticeable that the brain and œsophageal ring, with their nerves, are identical in shape in the two species, there being apparently but very little difference, externally, or internally, in the species of Limulus, both living and extinct.

The central nervous system consists of an œsophageal ring formed by the consolidation on each side of the œsophagus of the six ganglia innervating the six pairs of cephalic appendages. The ring is closed in front by the supra-œsophageal, or to speak more correctly, the pre-œsophageal ganglia or brain; the brain is the partial homologue of the supra-œsophageal ganglia of other Arthropoda.

It will be remembered that in other arthropods the brain is situated in the upper part of the head, in a plane somewhat different in direction from that of the rest of the ganglionic cord. In the Arachnida the supra-œsophageal ganglion also is in a different plane from that of the œsophageal mass, forming a small, more or less bilobed subspherical mass resting directly over and upon the front part of the œsophageal nerve-mass or œsophageal ring. In Limulus, however, as seen by Fig. 1 (in the text), the flattened subovate brain is situated directly in front of and in the same plane as the œsophageal ring and also the abdominal portion of the central nervous system.

Hence the position of the brain is pre-œsophageal rather than supra-œsophageal. The brain

* For references to the works of this and of other authors see the bibliography at the end of this article.

is separated from the œsophageal ring by a slight but yet distinct constriction seen both above and beneath, the constriction on the upper or dorsal side passing just behind the lateral eye-lobes, viz., those sending nerves to the large lateral compound eyes. It is broader at the base than it is thick, and narrow in front, seen from above, so that it is about a fourth narrower in front (in front of the origin of the lateral-eye nerves) than at the base or posterior end.

The ventral or under side is quite regularly convex and fuller and rounder than above; the convexity or fullness is greater in the center and drops or extends down considerably below the origin of the nerves of the first pair of appendages, this being the portion below the central lobes and which is filled with the ruffllelike masses of small, ganglionic or chromatic cells.

The brain of a Limulus about 10 inches long, exclusive of the caudal spine, is about 6 mm. in diameter; it is conico-spheroidal, broad and flattened from above, and on the under side full

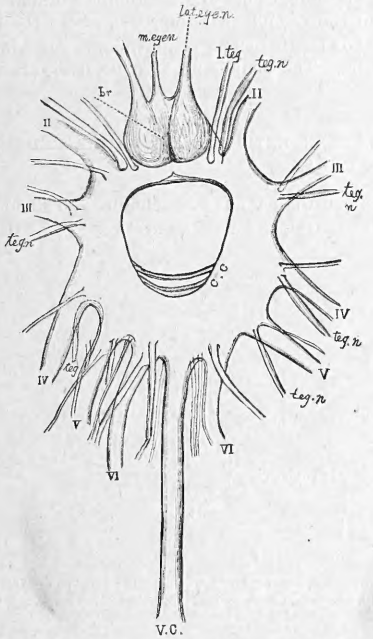

FIG. I. Brain and œsophageal ring of Limulus, seen from above; *br.*, brain; *cc.*, commissures behind the œsophagus; *m. eye n.*, median-eye nerve; *lat. eye n.*, lateral-eye nerve: I–VI, nerves to the six pairs of cephalothoracic appendages or legs; *v. c.*, ventral cord; *l. teg.*, lower tegumental nerve; *teg. n.*, other tegumental nerves.

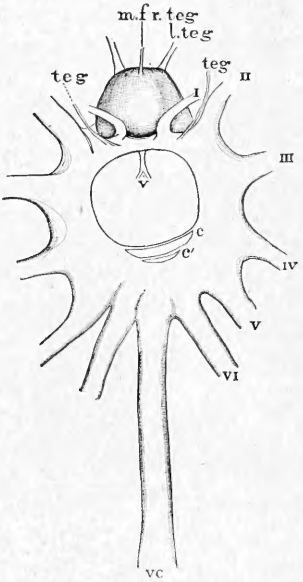

FIG. II.—Ventral view of the brain and œsophageal ring of Limulus. *m. fr. teg.*, medio-frontal tegumental nerve; *b. teg. n.*, lower tegumental nerve or nerve to the sensorial pit. Author del.

and rounded; on the upper side is a broad, shallow, median furrow, indicating that it is double. In the young Limulus, with a body about 2 inches long, exclusive of the caudal spine, the brain is longer, narrower, and less spherical.

Three pairs of nerves and a median unpaired one (the ocellar) arise from the upper third of the anterior face of the brain. The two lateral-eye nerves are the largest, arising very near the upper side of the brain, one on each side of the median furrow, so that the second and third sections made by the microtome pass through them. Next below (from above downwards) is the origin of the single nerve sent to the two ocelli. We have not traced this nerve as far as the ocelli, but Milne-Edwards states that near the ocelli it divides into two branches. On each side

of the ocellar nerve, and in nearly the same plane, arise two tegumental nerves, and directly below them a second pair of longer nerves (fronto-inferior tegumental of Milne-Edwards) descend ventrally. No nerves arise from the inferior half or two-thirds of the brain, which is smooth and rounded, with no indications of a median furrow. There is also an unpaired mediofrontal nerve.

It will then be seen that, as stated by A. Milne-Edwards, there are no antennal nerves, such as usually exist in anthropods with the exception of the Arachnida. This we have proved in the same manner as Milne-Edwards (though at the time ignorant that he had pursued the same method), by laying open with fine scissors the envelope (arterial or perineurial) which reaches to the posterior end of the brain and seeing that the fibers of the nerves sent to the first pair of appendages originate quite independently of the brain itself. Moreover, after making sections of several brains, it is easy to see that only the commissures connecting the brain with the œsophageal ring are present, the nerves to the first pair of appendages not arising from the brain itself, but from the anterior and outer part of each side of the œsophageal ring, *i. e.*, where the ring joins the brain. It is to be observed that the nerves of the first pair of appendages arise in the same plane as those of the second and succeeding pairs. The commissures (connectives) are very short in the larva and obsolete in the adult.

III. THE MORPHOLOGY OF THE BRAIN OF LIMULUS SEEN EXTERNALLY AS COMPARED WITH THAT OF ARACHNIDA.

The brain of Limulus is a very primitive one, more so than that of Arachnida, and should be in this respect compared with that of the crustacean Branchipus. It is an *archicerebrum*,* to use

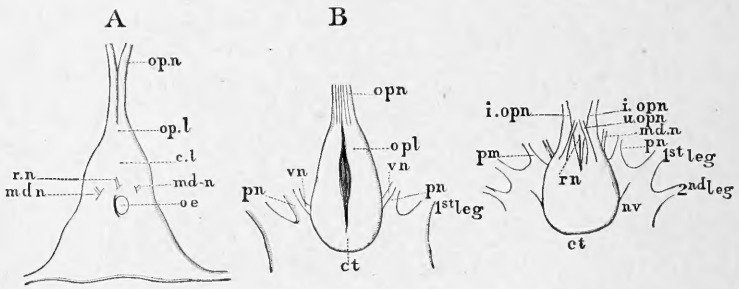

FIG. III.—A, brain of Phalangium; B, brain of Lycosa; C, brain of Epeira; *op. n*, optic nerve; *op. l*, optic lobe; *c. l* (and *ct*) cerebral lobe; *md. n*, mandibular nerve; *r. n*, rostral nerve; *oe*, œsophageal ring; *vn* (and *nv*), visceral nerve; *pn* (and *pm*) pedipalpal nerve; *i. opn*, lower optic nerve; *u. opn*, upper optic nerve.—After St. Remy.

the term proposed by Lankester. It sends nerves to the eyes alone and none to the appendages. As we shall see in the course of our essay it is composed of optic lobes alone, together with the cerebral lobes and their nucleogenous or mushroom bodies. This primitive condition places it only slightly above the grade of that of Peripatus.

It may be observed that even within the limits of the Crustacea there is a great range of variation in the constitution of the supra-œsophageal ganglion. The simplest condition, that in which the Crustacean brain is almost directly homologous with that of annelids, is to be found in the brain of the phyllopods (Limnetidæ and Branchipodidæ), where the diminutive brain is composed of the optic and cerebral ganglia alone, the brain of these forms being the most primitive to be found in arthropods. In these brains no antennal ganglia occur; they are situated behind the brain. The next step is seen in Apus, whose brain, contrary to Lankester's assumption, has been

* The terms syncerebrum and archicerebrum appear to us to apply to very different kinds of brain. The archicerebrum of Branchipus, for example, is a very different organ from that of Limulus, both histologically and morphologically. That of Branchipus is simpler and more wormlike than that of Limulus.

proved by Pelseneer to contain the antennal ganglia, though the nerves branch off at a considerable distance from the brain, on the side of the œsophagus. A step higher is seen in the brain of isopods, where, as we have described and figured* the first and second antennal ganglia of Asellus are not closely coalesced and consolidated with the optic and cerebral lobes, but are separate from the brain and situated below and posterior to it, though in front of the œsophagus. The most complex type of crustacean brain is that of the highly specialized Decapoda.

The brain of adult insects is on the same high plane as that of decapod crustacea, the optic and antennal lobes being invariably coalesced with the cerebral, the whole mass being separated from the infra-œsophageal ganglion, and so it is with the brain of myriopods.

The Arachnidan brain is very distinct in its external appearance from that of insects or crustacea.

Prof. Patten† has given us what is apparently a clear and accurate figure on an enlarged scale of the scorpion's central nervous system, which we take the liberty to copy, with a change in position and consequent change in the lettering.

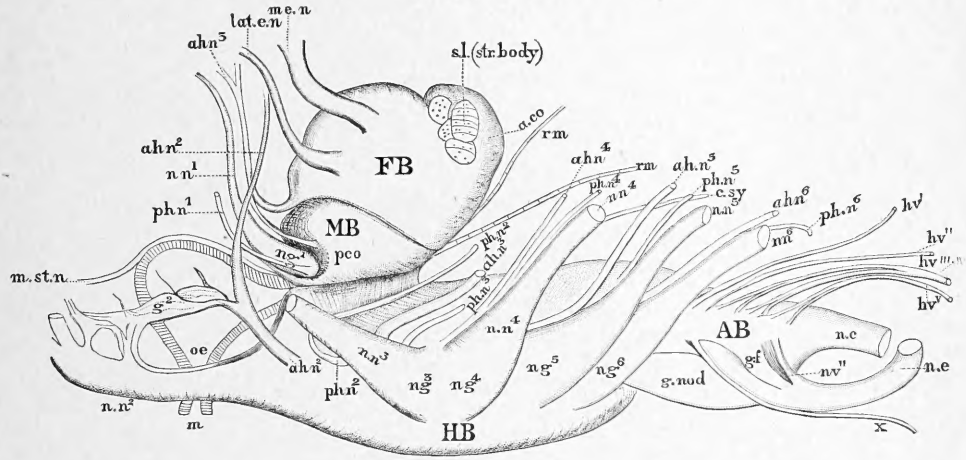

FIG. IV.—Brain of adult scorpion, constructed by means of sections and dissections. A. B., accessory brain; H. B., hind brain; M. B., mid brain; F. B., fore brain; *a. co.*, anterior commissures; *a. h. n.* 1-6, anterior hæmal nerves of the thoracic neuromeres; *c. sy.* cranial sympathetic (?); g^2, large ganglion derived from the segmental and coxal sense organs, and giving off many branches to the scattered sense organs in skin of chelæ; *g. f.*, ganglion fusiforme; *g. nod.*, ganglion nodosum or g. striatum; *h. n. s.*, a very delicate root, probably representing the hæmal nerve of the third fore-brain neuromere, partially fused with the hæmal nerve of the cheliceral segment; *h. v.'* and *h. v.''*, the independent anterior and posterior nerves of the first vagus neuromere; *h. v.*^{iii} and *h. v.*^{iv}, the four partially fused hæmal nerves of the second and third vagus neuromeres; *lat. e. n.*, lateral-eye nerve; *m*, mouth; *me. n.*, median-eye nerve; *m. st. n.*, median stomodæal rostral nerve; *n. e.*, comb or pectinal nerve; *ng.*1-6, neural ganglia at the base of the neural nerves; *n. n.*1-6, neural nerves of the thoracic segments; *h. v.*1-4, roots of the neural vagus nerves; *ph. n.*1-6, posterior hæmal nerves of thethorax; *p. co.*, posterior brain commissure; *s. l.* (str. body), semilunar lobe or first brain segment; *r. m.*, retractor muscles to œsophagus.—After Patten.

Prof. Patten incorrectly applies the term "brain" to the entire central nervous system, only excepting the abdominal ganglia, dividing the brain and œsophageal ring or mass into three divisions, viz, the fore, mid, and hind brain, as indicated in his figure. But restricting the term brain to the supra-œsophageal ganglionic mass, it will be seen that the ganglia which innervate the first pair of appendages, though separate in the embryo, are in the adult scorpion closely united with the brain, though there is a slight constriction between the two portions of the brain, viz, between the "mid brain" (or rostro-mandibular ganglion of St. Remy) and the "fore brain."

It is desirable also, for the sake of clearness, not to consider the "hind brain" as a part of the brain, since it is a post-œsophageal mass, innervating the cephalic and thoracic appendages,

*Structure of the brain of sessile-eyed Crustacea.

†Quart. Journ. Micr. Sc., 317, 1890.

viz, the mouth-parts and the four pairs of legs. No author, so far as we are aware, but Patten, has extended the term brain to include the post-œsophageal mass, and he apparently does this in order to carry out his fancied homology of the scorpion's central nervous system with the brain and spinal cord of vertebrates.

St. Remy has in a masterly way described the brain of the higher Arachnida (Phalangidæ, Spiders, and Scorpions), restricting the term brain to two regions, the first of which he calls, after Schimkewitsch, the "optic ganglion," which furnishes the optic nerves only. (St. Remy's term "optic ganglion," which is not a happy one, since the same name has been used by nearly all authors for the optic ganglion of insects and decapod crustacea, viz, the mass of cells situated between the optic lobes and the optic nerves, should be designated by the general name supra-œsophageal ganglion.*)

According to St. Remy, this region comprises "three perfectly characterized parts in all the types which we have studied, the optic lobes, the posterior stratified organ, and the cerebral lobes." The second region of the brain, which St. Remy† designates the rostro-mandibular ganglion, is the midbrain of Patten. This portion, then, innervates the first pair of appendages of Arachnida and also the rostrum, which St. Remy regards as the homologue of the labrum of insects and crustaceans.

We hold the view that the brain, or pre-œsophageal ganglionic mass, or prostomial nervous centers of Limulus, is not the homologue of the brain of Arachnida, but only represents the first region of it, the optic ganglion of Schimkewitsch and of St. Remy, and the forebrain of Patten. It lacks the rostro-mandibular ganglion of the arachnid brain, this ganglionic mass being fused with the œsophageal ring and more intimately united with it than with the brain. Thus the brain of Limulus is simpler, more primitive, and, in this respect, more like that of Peripatus and Annelids than is that of Arachnida.

We hope to show that this can be proved not only by gross dissection of the adult, but by the facts and figures which we give in this paper.

For the adult brain can be readily dissected from the œsophageal ring without cutting into the brain, and as will be seen in my figures of the horizontal sections of the brain (see especially Pl. VI, Fig. 1, and Pl. V, Figs. 20–22, *g. app'*), the mass of ganglionic cells supplying the nerves to the first pair of appendages are behind and outside of the brain proper.‡ The division can also be seen in the entire brain, and also in Milne-Edwards figures. Moreover, the embryonic and larval conditions prove that the rostro-mandibular region in Limulus belongs with the œsophageal ring.

Viallanes, in his admirable memoir on the brain of the locust (Annales Sc. Nat., p. 1, 1887), has proposed a new classification of the parts of the brain.

He divides the brain of insects and of crustacea into three segments, *i. e.*, the *protocerebrum* (brain of the first zoönite); the *deutocerebrum* (brain of the second zoönite), and the *tritocerebrum* (brain of the third zoönite).

*The term supra-œsophageal ganglion is an inexact one, as in reality it is composed of from two to four pairs of ganglia, which are separate in the embryo, becoming consolidated in the adult. The term supra-œsophageal ganglionic mass, or prostomial ganglionic mass, would be more exact, unless a briefer single word could be suggested; meanwhile the term *brain* is sufficient for ordinary use, only bearing in mind that this organ varies in the number of primitive lobes in different classes of Arthropoda.

†La seconde région du cerveau, que nous avons désignée sous le nom de *ganglion rostro-mandibulaire*, a une constitution beaucoup plus simple et, par suite, beaucoup plus semblable dans tout le groupe. Elle se compose d'une masse nerveuse, traversée par le tube digestif, dont la portion sus-œsophagienne se divise en avant en trois lobes, un impair, très petit, d'où part sur la ligne médiane le nerf du rostre, et deux autres plus volumineux, disposés latéralement, qui donnent naissance aux nerfs des chélicères. Ceux-ci forment une seule paire chez les Phalangides et chez les Aranéides où nous les avons vus se diviser bientôt en deux branches; il y en a deux paires chez les Scorpionides, les deux nerfs de chaque côté correspondant vraisemblablement aux deux branches de division du tronc unique des Aranéides. Le ganglion rostro-mandibulaire donne naissance, dans ce dernier groupe, à une paire de nerfs viscéraux. (P. 230.)

‡Different anatomists have taken different views of this subject. Dohrn remarks: "Bei Limulus aber wird nur das vorderste Paar der Gliedmassen von dem oberen Schlund-ganglion versagt; die übrigen empfangen ihre Nerven aus der Bauchganglienkette," p. 585. On the other hand Lankester remarks: "In the first place the brain and œsophageal collar of Scorpio are more intimately fused with one another than are the corresponding parts of Limulus," and adds further on: "From the collar, then, in Scorpio as in Limulus, the nerves to all six of the pediform appendages take their origin." ("Limulus an Arachnid," pp. 9 and 10).

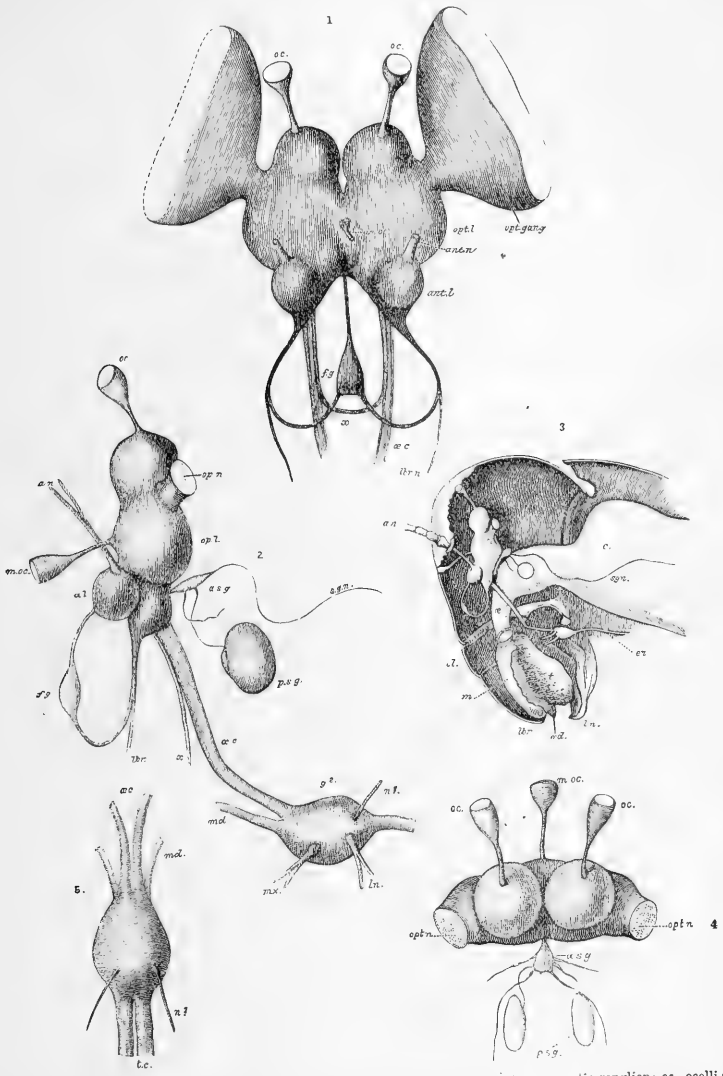

FIG. V.—*Brain of the locust.* 1. Front view of the brain of *Caloptenus femur-rubrum*: *opt. gang.*, optic ganglion; *oc.*, ocelli and nerves leading to them from the two hemispheres, each ocellar nerve arising from the region containing the calices; *m. oc.*, median ocellar nerve; *opt. l.*, optic lobe sending off the optic nerve to the optic ganglion; *ant. l.*, antennal or olfactory lobe; *ant. n.*, antennal nerve; *f. g.*, frontal ganglion of sympathetic nerve; *lbr. n.*, nerve to labrum; *x*, cross-nerve or commissure between the two hemispheres; *œ. c.*, œsophageal commissure to subœsophageal ganglion. 2. Side view of the brain and subœsophageal ganglion (lettering of brain as in Fig. 1): *s. g.*, stomatogastric or sympathetic nerve; *a. s. g.*, anterior, and *p. s. g.*, posterior, sympathetic ganglia; *g.* 2. subœsophageal ganglion; *md.*, nerve to mandible; *mx.*, maxillary nerve; *ln.*, labial nerve; *n.* ?, unknown nerve, perhaps salivary? 3. Interior view of the right half of the head, showing the brain in its natural position; *an.*, antenna; *cl.*, clypeus; *lbr.*, labrum; *m.*, mouth cavity; *md.*, mandible; *t.*, tongue; *œ.*, œsophagus; *c.*, crop; *en.*, right half of the endocranium or X-shaped bone, through the anterior angle of which the œsophagus passes, while the great mandibular muscles play in the lateral angles. The moon-shaped edge is that made by the knife passing through the center of the X. 4. View of brain from above (letters as before). 5. Subœsophageal ganglion from above: *t. c.*, commissure to the succeeding thoracic ganglion; other letters as before. Fig. 3 is enlarged eight times; all the rest twenty-five times.

Drawn from original dissections by the late Mr. Edward Burgess.—From Second Report U. S. Entomological Commission.

He finds in the *protocerebrum* of the insect (locust, etc.) all the constituent parts of the protocerebrum of crustacea. These are the layer of postretinal fibers, the ganglionic plate, the external chiasma, the external medullary mass, the protocerebral lobe, the ocellar nerves and lobes, the bridge of the cerebral lobes, and the middle (central) protocerebrum.

The *deutocerebrum* comprises the olfactory antennal lobes, and the dorsal lobe of the deutocerebrum. The deutocerebrum gives origin to four pairs of nerves, *i. e.*, (1) the antennary nerves; (2) the accessory antennal nerves; (3) the tegumental nerves; (4) the root of the stomatogastric ganglion.

The *tritocerebrum* is formed of a pair of lobes (tritocerebral lobes), which are united by a transverse commissure passing under the œsophagus. The lobes give origin to a nervous trunk, which is divided into two branches, *i. e.*, the labral nerves, and root of the frontal ganglion.

Dr. Saint Remy adopts Viallanes' classification, but he concludes that in Myriopoda the brain is divided into the "three ganglions which are perfectly comparable to the brain of the higher crustacea and of insects, though their structure is infinitely more simple." But in the brain of Arachnida he finds only the protocerebrum, and adds: "*Mais pour ce qui est de la seconde région du cerveau, ou ganglion rostro-mandibulaire, la détermination des homologies est plus délicate.*" The deutocerebrum of the insects, myriopods and crustaceans "*n'est pas représenté ici.*" He thinks that the rostro-mandibular ganglion of Arachnids is the homologue of the third region or tritocerebrum.

The shape and relations of the brain of insects is well shown by Fig. V.

Coming to Limulus we shall see that the brain does not include the rostro-mandibular ganglion found in spiders and scorpions, and that neither the tritocerebrum or the deutocerebrum is found, the brain representing the protocerebrum alone; or if the deutocerebrum is present it is not preœsophageal and is not yet fused with the archicerebrum.*

IV. Histology.

The histological elements of the brain of Limulus are closely similar to those of the Arachnidan brain, so ably described by Saint Remy. As in other Arthropods the histological constituents of the brain are the large ganglionic cells with abundant protoplasm, the punctuated or myeloid substance, the nervous fibers which form the origins or roots of the nerves, and the small ganglionic cells or nuclei.

These last-named cells unite to form certain bodies, the real nature and homology of which has made the study of this subject especially difficult. Indeed, the most striking feature of the brain of Limulus are what we called in our former memoir the convoluted, ruffle-like "nucleogenous bodies." They form cortical layers enveloping the cerebral and optic lobes, and where scattered inclose masses of fine fibrillar and myeloid or punctuated substance. These bodies appear at first sight to be composed of closely crowded nuclei, but when they are scattered they are seen to be small ganglionic cells. They appear to be the "ganglionic nuclei" (*ganglïösen Kerne*) of Dietl† (p. 303, etc.) which he also refers to as "free protoplasmaless nuclei" (p. 496). See also Dietl's later paper (1878), where he thus defines these ganglion cells: "4. Kleine Zellen mit sehr schmalen Protoplasmasaum der trübe Nucleus enthält Nucleoli (Sinnesanschwellungen)," p. 14.

I also regard them as identical with the "*cellules chromatiques*" of Saint Remy. He describes them as "unipolar cells, so poor in protoplasm that their cellular outlines escape observation in sections," and adds: "Besides the extreme reduction of the protoplasmic body these elements present a remarkable peculiarity: the richness of their nucleus in chromatic substance capable of taking very distinctly the coloring matters, even after the prolonged action of osmic

* The terms protocerebrum, deutocerebrum, and tritocerebrum are rather cumbersome, and as they represent three distinct pre-œsophageal segments (arthromeres), it seems to us more convenient to call the protocerebrum the optic segment or division of the brain, because the principal lobes composing it are those sending nerves to the compound eyes and ocelli; so also the deutocerebrum might be denominated the antennal segment, and the tritocerebrum the labral segment. This nomenclature would well accord with the names mandibular, and first and second maxillary segments situated behind the mouth, the ganglia contained in them being called by the same names, mandibular, etc.

† Die Organization des Arthropodengehirns.

acid. Finally, what renders them specially interesting is that we only meet with them in the sensorial centers of the brain, where they form very dense masses. These elements are abundant in the Myriopods, where they are especially small and brightly colored; they likewise occur in the Arachnids and Onychophores. They are always in direct relation with the differentiations of the punctuated substance, and, in a general way, we have stated that they are far more numerous and present characters far more trenchant where the brain is higher in organization. Thus in the Myriopods they are especially abundant in the complicated brains of Julus and of Scutigera, and do not exist in the rudimentary brain of Geophilus. In the Arachnids we notice their presence in the highly developed optic lobes of Lycodids or of Phalangids, while they are replaced by small, less deeply stained nucleated cells and with visible protoplasm in the very simple lobe of Agalenids, or even by ordinary cells in the rudimentary lobe of the Pholcids." He calls these cells "*cellules chromatiques*," in reference to one of their salient characters, and we shall often use this term for those of Limulus, though rather preferring the name aprotoplasmic cells or small ganglion cells.

These small, aprotoplasmic, unipolar ganglion cells as contrasted with the large ganglion cells are represented in Pl. XII, fig. 6*a*, *smgc*, where their size as compared with the ordinary large ganglion cells is well brought out.

They are seen to be much smaller than the nuclei of the large ganglion cells, and their nuclei have usually two or three nucleoli, though the number may vary from 1 to 6. In the large ganglion cells the number of nucleoli varies from 1 to 4, there being usually two more distinct than the others.

In this ganglion, that of one of the median eyes, the fibrilla from each of the unipolar chromatic or aprotoplasmic ganglion cells is seen entering the tangled central white mass, and among the convoluted masses of fibrillæ are seen irregular masses of myeloid substance.

This myeloid or punctuated substance, common to the central white fibrillar substance of all Arthropod brain ganglia, and usually enveloped by the ganglion-cells, we have referred to as follows in our essay on the structure of the brain of the sessile-eyed crustacea:

The *punktsubstanz*, *marksubstanz* or myeloid substance, as we may designate it, differs in its topographical relations from that of the brain of Decapoda. This myeloid substance, which seems to be peculiar to the worms, mollusks, and especially the crustacea and insects, has been most thoroughly studied by Leydig. This is the central finely-granular part of the brain, in which granules have short irregular fibers passing through them. In his *Vom Bau des thierischen Körpers*, p. 89, Leydig thus refers to it:

"In the brain and ventral ganglia of the leech, of insects, and in the brain of the Gastropods (Schnecken) I observe that the stalks (stiele) of the ganglion-cells in nowise immediately arise as nerve-fibers, but are planted in a molecular mass or *punktsubstanz* situated in the center of the ganglion, and merged with this substance. It follows, from what I have seen, that there is no doubt *that the origin of the nerve-fibers first takes place from this central punktsubstanz*.

"This relation is the rule. But there also occur in the nerve-centers of the invertebrates single definitely situated ganglion cells, whose continuations become nerve-fibers without the intervention of a superadded punktsubstanz."

Leydig subsequently (p. 91) further describes this myeloid substance, stating that the granules composing it form a reticulated mass of fibrillæ, or, in other words, a tangled web of very fine fibers:

"We at present consider that by the passage of the continuation of the ganglion cells into the *punktsubstanz* this continuation becomes lost in the fine threads, and on the other side of the *punktsubstanz* the similar fibrillar substance forms the origin of the axis-cylinders arranged parallel to one another; so it is as good as certain *that the single axis-cylinder derives its fibrillar substance as a mixture from the most diverse ganglion-cells*."

The brain of Limulus is, as we have seen, composed of three pairs of ganglia, viz, the lateral optic lobes, the median optic lobes, and the cerebral lobes with their offshoots, the pair of mushroom bodies. We will begin our account of the topography of the brain with the first of these.

V. The Lateral-Eye Lobes or Ganglia.

(Pls. I, II, VI, VII, IX, XI.)

These are recognized without much difficulty, and are situated at the uppermost part of the brain, the convex contour of their anterior portion being visible from a surface view without a lens. The lobes are situated a little behind the middle of the brain, and are placed rather far apart, situated one on each side of the brain, there being a well-marked valley or depression between them. The brain seen from above is, then, slightly bilobed, but not so markedly so as in Arachnida. The two lateral-eye nerves arise from the lobes at a point considerably behind the

origin of the unpaired median-eye nerve, and nearly opposite the position of the median-eye lobe. The anterior division of the lobe* is rounded, somewhat pear-shaped, and more than twice as thick as the base of the nerves to which it gives rise (Pl. I, Fig. 2). Each lobe is mostly made up of a tangled mass of nerve fibers proceeding from small ganglionic cells (chromatic cells) buried in the mass of the lobe (Pl. I, Figs. 1, 2, Pl. II, Figs. 7*a*, 7*b*; and young, VI. Fig. 1, Pl. VII. Fig. 2, which represents the entire lobe, and forming an irregular cylindrical sheet, or plate, passing through the lobe.† This layer is not, then, wholly a cortical one, but is in part internal, and may be called the chromatic-cellular layer of the lobe, and penetrates the lobes from beneath, being an offshoot from the mass of chromatic-cell layers impinging upon or partly enveloping the lower side of the lobes, as seen in Pl. VI, Fig. 1, *ch. c. layer*. In the young Limulus this layer is more external and cortical. These cells differ from the ordinary large ganglionic cells in having very little protoplasm enveloping the nucleus, the latter taking a deep stain, and thus being very distinct, while the nuclei take the carmine stain well. They might be called aprotoplasmic ganglion-cells. These cells appear to be identical with Saint Remy's chromatic cells. Many of these cells are scattered through the center of the lobe, especially in the lower portion. We shall refer to them as chromatic cells, or aprotoplasmic or small ganglion cells. We are not entirely satisfied with the term chromatic cells, as this does not describe their more fundamental nature or their small size. Similar chromatic cells are scattered throughout the inner aspect of the lobe, between the periphery and the chromatic-cell layer within.

These chromatic cells are plainly seen in the section represented by Pl. II, Figs. 7, 7*a*, to be unipolar and to give off the fine fibers which form the tangled fibrillar mass constituting the greater part of the lobe. But besides these fibers throughout the tangled mass are to be seen irregular masses of the white myeloid or punctured substance (*punktsubstanz*) which appears to form a sort of network extending throughout the central part of the lobe. (See also Pls. XXI–XXIV, made from Dr. Gray's excellent photographs.)

As already stated, the space directly under the lateral-eye lobes is occupied with the ruffle-like masses of the mushroom bodies passing up from the middle on each side of the brain (Pl. I, Figs. 2, 5), and branches from the cortical mass of these ruffle-like plates or sheets envelope the lower and outer sides of the lateral optic lobes, until, as represented in Pl. I, Fig. 5, the lobes have disappeared and their place is taken by the chromatic-cell layers. Layers of chromatic cells also appear in front between the lower faces of the lateral-eye lobes, as in Pl. VII, Fig. 2. The lower face of the lobes are thus seen to be partly enveloped by layers of chromatic cells.

The question now arises, have these layers of chromatic ganglion-cells forming in part the cortex of the lateral-eye lobes any homologues in the brain of Arachnida? Without having any sections of the brain of spiders with which to compare them, I am disposed to regard them as possibly identical with the *lame glomérulée* of the interior eye-lobe of Lycosa, etc., described by Saint Remy. (See his Pl. VII, Figs. 72–76, and Pl. VIII, Figs. 86–88, *l. gl.*) But until direct comparison be made between these structures in actual sections, it will be difficult to decide this point. Judging by Saint Remy's figures alone, they appear to be similar, but I have been unable to find the glomerules and nervous tubes described by him. At present the chromatic-cell layer of the lobes under consideration appear to me to be simpler in structure and less differentiated than in Arachnida. I have also been unable to detect any bodies homologous with the "medullary plates" of Saint Remy, and which form so characteristic a feature of the upper and lower optic lobes of the brain of Arachnids. In apparently lacking these highly specialized structures the brain of Limulus appears to be more primitive.

* This portion of the lobe is the *lame ganglionnaire* (*lg*) of Viallanes, who divides the optic ganglion into three masses, the most anterior being the "ganglionic plate or sheet, (*lame*). This sheet or mass is connected with the second mass (*me* of Viallanes' plate 10, Fig. 17)" by a bundle of chiasmic fibers or "external chiasma" (*che*). The third mass (*mi*) is "united with the cerebral lobe (*lc*) by a short peduncle like the optic tract of Crustacea and Insects" (p. 415). These two posterior masses are represented in my Pl. II, Figs. 8, 9, and 10, *l. eye.* l^1 and *l. eye.* l^2; Pl. VII, Fig. 2. I had regarded them as connected rather with the cerebral lobes than with the optic lobes, but now accept Viallanes view as to their true relationship.

† This layer is figured by Viallanes in his Pl. 10, Fig. 77, but not described. Pl. VII, Fig. 2*a*. *e. ch.* represents the "external chiasma" (*sic*) discovered and so named by Viallanes and fairly well seen in my sections.

VI. The Median-Eye Ganglia or Lobes.

(Pl. I, Figs. 5–7, II, Figs. 8, 9, 10; Pl. III, Fig. 11, VII, Figs. 1, 2.)

After passing, in horizontal sections, down through the lateral-eye nerves and lobes the knife cuts through the origin of the median-eye nerves and the lobes or ganglia from which they originate.

These lobes are, in the adult brain, situated considerably below the plane of the lateral-eye lobes, and the origin of the bundle of nerve-fibers leading to the median-eye nerve is difficult to detect, owing to the fact that, so far as our sections show us, they are small, slender, quite irregular in shape, not being regularly pear-shaped or subspherical, and their fibers appear to be more or less continuous with the fibers of the cerebral lobes; in fact, they at first sight appear to be branches of the inner portion of the fibrous matter of the cerebral lobes. The two median-eye nerves being blended, within the brain as well as without, only dividing near the median eyes themselves, their cortical cells are also near together and not separated into distinct areas. I have had no sections either of the young or adult animal which have clearly shown the mode of origin of the fibers forming the origins or roots of the nerves, from any large ganglion-cells. The ganglia are more or less blended or coalesced with the cerebral ganglia, and I believe it will be difficult, if not impossible, to make them out unless we examine sections of the young after the first molt, or when about half an inch in length, exclusive of the caudal spine.*

I have been able to trace the origin of the median-eye nerve into the central part of the brain to the point *m. eye n.* in Pl. III, Fig. 11, and it appears probable that the large ganglion-cells which give origin to a part of the median-eye nerve are associated more or less intimately with those which supply the fibers, or a part of them, to the inner aspect of the cerebral lobes. We will, however, consider the large ganglion-cells, to be seen in the section represented at *m. eye gang.*, Pl. III, Fig. 11, as belonging to the median-eye lobe. This area of large ganglion-cells, with smaller ones intermingled, is bilateral, the cells being arranged irregularly on each side of an irregular and very slightly marked median line which is clear of them.

We will now describe the sections passing through the blended median-eye nerves, and the double lobe from which the double nerve originates. In Pl. II, Fig. 8, the knife has passed through the middle of the median-eye nerve (*m. eye n.*). The nerve fibers from it pass in towards the middle of the brain and partially fuse with two masses (Pl. II, Fig. 9, *m. eye l.*) which appear as two horns or offshoots of the fibrous portion of the lateral-eye lobes. The triangular space between these two roots of the median-eye fibrillar masses is bounded posteriorly by the cerebral commissure (*c. com.*). The ganglion-cells scattered through this mass are arranged on each side of the obscurely-marked median line of the brain. As in this plane of the brain I can perceive no fibers from any of these ganglion-cells entering into the cerebral lobes, I take it that the cells in question send their fibers into the median-eye lobes and help build up the median-eye nerve. The fibers of the latter are also, with little doubt, reënforced with fibrillæ from the masses of chromatic or small ganglion-cells which envelop the nerve just before it passes out of the brain.

In Pl. III, Fig. 11, the cerebral commissure is complete, and what seems the right root of the median eye nerve is seen to penetrate farther into the center of the brain than in the two sections immediately above. In Pl. III, Fig. 12, the knife has passed just below the roots of the median eye nerve and the cylindrical plates or sheets of small ganglion or chromatic cells nearly meet under the nerve. This is also seen in Pl. III, Fig. 13, while in the section represented by Pl. III, Fig. 14, there are no traces of the median eye nerve, the ruffle-like cylinders of small ganglion cells being now crowded together under where the nerve passes out of the brain.

The relations of the median-eye lobes are well shown in the sections of a small Limulus, represented by Pl. VII, Figs. 1 and 2. In Fig. 1 is seen the horseshoe shaped bundle of fibers, inclosing the

*The limits of the fibrous portion of these lobes have been clearly distinguished by Viallanes (p. 416 and his Pl. II, Figs. 3 and 5, *loc.*, though in his model he does not represent the central mass of large and small ganglion cells. I now see that my Pl. VII, Figs. 1 and 2 represents the ganglia in question. It is the blending or fusion of the portions of these and the lateral-eye lobes adjacent to the cerebral lobes, which has rendered it so difficult for me to obtain a clear idea of their limits. In this respect the brain of Limulus differs remarkably from that of Crustacea or Insects, as well as Arachnida.

mass of large and small ganglion cells, with the roots of the fibers to which they give origin. The cellular mass belonging to each lobe is seen to be separated by a median space free from ganglion cells. (This large mass of cells, forming the bulk of each lobe, does not appear to be represented by Viallanes either in his figures of actual sections or of his wax model, and they form much larger and more bulky masses than he describes or figures.) In the section represented by Fig. 2, the roots of the median-eye nerves (*m. eye n. r.*) are seen on their outer aspect to be fused with the proximal end of the lateral-eye lobes.

Fig. 2*a* represents the bundle of twisted fibers forming the "external chiasma" of Viallanes; these fibers appear to end in irregular pear-shaped masses of punctured substance, and beyond them is the zone of internal chromatic cells (*ch. c. l.*). In Pl. VI, Fig. 1, at f' is seen on each side a fascia arising from the large ganglion cells in the lower part of the median-eye lobe, passing back into the cerebral lobes, and behind is a second fascia (f'').

VII. The Cerebral Ganglia or Lobes.

(Plates III, IV, V, 20, 21, VI, VII, VIII.)

The third and much the largest pair of lobes are the cerebral ganglia. They comprise the bulk of the brain when we take into account the masses of small ganglion cells constituting the "*corps pedonculé*" of Viallanes. The central fibrillar or white portion of these ganglia are very irregular in outline compared with the massive, more or less spherical cerebral lobes of the Arachnida; and the cortical masses of small ganglion cells which enclose and also ramify through the cerebral white mass are very different in disposition from the ganglionic cortex of the Arachnidan brain, and they are enormously developed in the brain of Limulus.

The white fibrillar portion of the cerebral lobes are arranged in two masses, one on each side of the median line of the brain. These lobes are very irregular in outline, slender, and apparently shrunken. They are narrow and thin, sending off irregular lateral lobules.* The cerebral lobes are connected posteriorly by a thick cerebral commissure (*c. com.*).

This commissure, as numerous sections show (Pls. II, Figs. 8, 9, 10; III, Figs. 11–13), consists of fibrillæ originating from the thin crescent-shaped central dense mass of small ganglion (chromatic) cells (*c. com. cortex*) near the posterior margin of the brain, and which overlies the median portion of the origin of the great commissures leading to the œsophageal ring.

The central or larger mass of the cerebral lobes does not pass much below the middle of the brain. It gives off the pairs of upper and lower tegumental nerves, and the posterior lobules, one on each side, serve as the origin of the great commissures connecting the brain with the œsophageal ring, which latter is originally formed by the coalescence of the neuromeres of the postoral cephalothoracic appendage-bearing segments.

In order to clearly bring out the relations of the cerebral lobes I will first describe the horizontal sections of the young Limulus when about 2 inches in length, exclusive of the caudal spine.

In a series of 43 sections the uppermost sections of the brain do not involve the fibrous matter of the cerebral lobes. The first fibrous portion encountered in cutting sections from above downwards are the two subparallel curved lateral-eye strands, Pl. VII, Fig. 1, *lat.-eye., n. r.*, which send fibers to the anterior horn or process of the median-eye lobes. Between these two strands is a thick, horseshoe shaped bundle of fibers, the incomplete circle opening anteriorly near the front of the brain, and inclosing two large groups of ganglion cells. These are the roots or origin of the median-eye nerves.

In the second section below the one just described (Pl. VII, Fig. 2) the knife passes through the lower part of the median-eye lobes and through the upper part of the cerebral lobes, but involving the larger central mass of the lobes. The œsophageal commissures are seen to be large and thick; the commissures are reinforced by the fibers sent off from the small group of large ganglion cells ($l\ g\ c'''$) (those on the other side, not seen in this section). There is also a group of large ganglion cells ($l\ g\ c'$) on each side of the base of the brain.

In or near the central part of the cerebral lobes, Pl. VI, Fig. 1, in the fourth and fifth sections below the one just described, the mode of composition of the fibrous portion of the lobes is seen.

*These lateral lobules are the second and third masses of the lateral-eye lobes, according to Viallanes.

From the numerous large ganglion cells on each side of the median line of the brain, between the roots of the median-eye nerves, is sent off an anterior bundle of fibers (*f'*) which passes in and across the fibrous portion of the cerebral lobes, the fibers of each bundle meeting in the middle, so as to inclose an incomplete circle; a second set of fibers (*f''*) behind the first is to be seen behind; and this is succeeded by the transverse fibers which originate from the base of the œsophageal commissures, these fibers in part originating from the basal masses of large ganglion cells (*l g c'*).

On the side of the main fibrous masses, scattered throughout the cortical plates of small gan, glion cells, are seen, as at *m. b.*, the sections of irregular lateral branches of the mushroom body-which pass upwards from the ventral portion of the brain. In this section are also well shown the relations of the ganglia of the first pair of appendages with the fibers from the œsophageal commissures traversing the mass of large ganglion cells, the latter sending backwards their fibers, but most of them sending fibers to form the nerves to the first pair of appendages (*1st app. n.*).

In the second cut below the section just described the knife passes through the lower border of the cerebral lobes, where the fibers are thrown together in tangled masses, arising from the groups of large ganglion cells on each side.

In the next cut the fibrous portion of the cerebral lobes is formed of two halves, which are bulbous at their base, and in front give rise to the lower tegumental nerves (Pl. VIII, Fig. 1, *l t n.*).

Just below this the knife passes through the scattered bundles of fibers or branches of the mushroom body passing up from the under side of the brain (Pl. VIII, Fig. 2).

The brain here largely consists of plates of small-ganglion or mushroom-body cells, with portions of the fibrous bundles on each side of the median line, which seem to give rise to the median tegumental or hemal nerve, *m. n.*, and larger fragments on the outer sides. Near the posterior end of the brain are two masses of large ganglion cells. Just below the section just described the knife passes through the plane below which no nerves are sent off, and below which there are no large ganglion cells. This plane is situated between the second and lower third of the brain, and below it the mass of the brain is made up of plates or sheets of small ganglion cells inclosing white or fibrous masses, which pass up and, uniting, aid in forming the white or fibrous lobes and lobules of the cerebral ganglia (Pl. VIII, Fig. 4). (These plates are the lobes of the mushroom bodies.)

Thus the fibrous portion of the cerebral ganglia are composed of fibers from the comparatively few large ganglion cells and the vastly more numerous and more minute fibers emitted from the small ganglion or chromatic cells forming portions of the mushroom bodies; whether the fibers from the large cells pass backwards continuously from the cerebral lobes through the ganglia composing the œsophageal ring, and unite with certain fibers from the said ring to form the abdominal cords, or not, is a question yet to be solved.

Some peculiarities are to be seen in the sections of the brain of the fully grown specimens (10 inches long, exclusive of the caudal spine) which are not to be observed, so far as our experience goes, in the smaller ones. These we will proceed to indicate.

Pl. II, Fig. 8, represents a section passing through the median eye nerve and its lobes (*m. eye n.* and *m. eye-lobe*) and the upper part of the cerebral lobes. The knife has passed through the ends of the cerebral commissure (*c. com.*), ensheathed, especially posteriorly, by the small ganglion cells; on each side of the central mass of large and small ganglion cells is the irregular branched mass of white fibrous substance, which is small in proportion to the enormously developed masses of small ganglion cells of the mushroom bodies, with their inclosed masses of fibrous and myeloid substance on each side. In two sections farther down, Pl. II, Fig. 9, the cerebral commissure is seen on the left side to be continuous with the white fibrous matter of the left cerebral lobe, and on the right side are seen a few large ganglion cells. In the next section below, the halves of the cerebral commissures are seen to touch each other (Fig. 10); while in two sections still lower down (Pl. III, Fig. 11), the commissure is complete, with its posterior cortical sheath of chromatic cells. The white, fibrous posterior region of the cerebral lobes is now larger, and the two lobes, united behind by the commissure, are anteriorly fused with the lobes of the lateral eyes (Figs. 11, 12).

Still lower down (Pl. III, Fig. 12) this section cutting through the upper tegumental nerves (*u. teg. n.*) the œsophageal commissure on the right side of the brain is involved. The white por-

tion of the cerebral lobes is now smaller. One of the sheets of small ganglion cells is seen on the left side to throw off a sinuous bundle of fibers to aid in forming the œsophageal commissure of the left side (*fasc.*); and a little within is seen on the same side a group of large central ganglion cells,

In the section represented by Pl. III, Fig. 13, the central masses of large ganglion cells, directly under the median-eye lobes are seen to send their fibers outward from the median line of the brain, and on the left side the sheets of small ganglion cells (*sm. g. c.*) are distinctly seen sending delicate fibers into the commissure. In a few sections lower down (Pl. IV, Fig. 16) the anterior region of the white or fibrous portion of the lateral-eye lobes has diminished, while the section passes through near the middle of the œsophageal commissures, this section also passing through the middle of the entire brain, just at the lower edge of the pair of fronto-inferior tegumental nerves (the nerves to the sensorial pit, of Viallanes). At *gc.* is seen a group of large ganglion cells, sending a bundle of fibers to aid in making up the œsophageal commissures.

Fig. 17 (compare the transverse sections, Pl. XIII, Figs. 10, 11) represents a section through the two groups of central and the lateral groups of cerebral ganglion cells; of the latter Fig. 18 is an enlarged view. On the right side is seen a portion of the stalk of the mushroom-body (*st. m. b.*). In a few sections lower down the large ganglion cells are seen to be unipolar and to send their fibers into the œsophageal commissures, and the small ganglion or chromatic cells are also seen sending their fibers into the commissure. Fig. 19 is an enlarged portion a few sections lower down, showing the bundle of fibers arising from the group of lateral cerebral ganglion cells.

Figs. 20 and 21 represent sections passing through the lower part of the cerebral lobes, where the central group of large ganglion cells is larger; at *l. gc.* is an unusually large ganglion cell with a very thick fiber passing from it into the commissure.

In a few sections below (Figs. 21, 22, 23) the large ganglion cells disappear, and also the commissures, the lower third of the brain passing below the level of the œsophageal commissures, and the mass being filled with the sheets of chromatic ganglion cells. (See Pl. XXXI).

The longitudinal (sagittal) sections of the brain (Pl. IX, X, Figs. 1–13, and Pl. XXXVI).—An examination of the figures on Pls. IX and X will show how large a proportion of the brain is occupied by the cortical masses of chromatic cells, which, in addition to their forming the sides of the brain, occupy the lower half of the central portion. In Pl. XX, Fig. 1, the cut through one side of the brain passes through the outside of the base of the lateral-eye nerves, and also shaves the nerve of the median eyes, but no large ganglion cells are involved, or the central fibrous substance of the cerebral lobes. In succeeding sections nearer the median line of the brain, as those represented by Pl. IX, Figs. 2, 4,* and especially 3, the relations of the lateral-eye lobes to the cerebral lobes are brought out, the two lobes being separated by a thick screen of chromatin-cell plates or sheets, with their inclosed masses of fibrillar and myeloid substance belonging to the mushroom bodies.

The relations of the cortical masses of large ganglion cells of the median-eye and cerebral lobes are to be seen in Pl. X, Fig. 11, the median-eye lobes being situated above and a little in front of the cerebral large ganglion cells. In Pl. VIII, Figs. 5, 6, 7, three longitudinal sections of the brain of the younger Limulus, which is larger and thinner than in very large specimens, are represented, one (Fig. 5) showing the lateral-eye lobe and nerve, this section passing through the œsophageal ring, while the other (Fig. 6) illustrates a section passing through the median-eye lobe and nerve, and also the cerebral lobe. This section may be compared with that represented by Pl. X, Fig. 11, of the large Limulus.

The transverse sections of the brain (Pls. XI–XVI and XXXII).—In the large adult Limulus the transverse sections show well the great amount of space taken up by the (more or less) cylindrical sheets of chromatic cells of the mushroom-bodies. In the anterior sections, involving the origin of the lateral-eye nerves, the sections represented by Pl. XI, Figs. 1, 2, 3, and 5, pass exclusively through the sheets of chromatic cells, which are thus seen to form not only the lower portion but also the anterior region of the brain. At Fig. 3 the lateral-eye lobe on the right side is involved.

In the sections behind these toward the middle of the brain the anterior region of the cerebral lobes is cut through, and the portions of the white or fibrous matter intersected are seen to be confined, as in Figs. 4 and 5, to the upper third of the brain.

* The figure (4) referring to this figure has been inadvertently omitted by the lithographer.

As the knife passes through the posterior region of the lateral-eye lobes it also cuts through the upper and anterior region of the median-eye lobes (Figs. 4 and 5).

In the next section figured, Fig. 6, the knife passed behind the lateral-eye lobes, involving the median-eye lobes, and also the anterior region of the cerebral lobes which send lobules into the lower part of the brain. The section, like all the others, being a little oblique, show the white fibrous matter on the right side penetrating to the bottom of the brain. Fig. 6*a* is an enlarged view of the central portion of the left median-eye lobe, showing the large ganglion cells, which are seen to vary much in size; and the small ganglionic or chromatic cells forming the semicircular sheet or plate, and inclosing the fibrous matter as well as the myeloid or punctured substance. The inner layers of aprotoplasmic or chromatic cells (small ganglion cells) are here seen to send their fibrillæ in toward the center of the mass inclosed by the cells.

These small ganglion cells contain usually more than one nucleolus—usually two or three—and I have counted in them from 1 to 6 nucleoli. The number of nucleoli in the large ganglion cells varies from 1 to 4, but there are usually two. These cells are seen to be unipolar and to send their nerve fibers directly across toward the group of cells in the opposite lobe, though no distinct commissure is thus formed.

In a few sections farther back the ganglion cells, both large and small, are arranged as in Pl. XI, Fig. 7, and Pl. XII, Fig. 8 shows their arrangement and relations to the central and lateral large ganglion cells in a section made still farther back, near the middle of the brain.

In the section represented by Pl. XII, Fig. 9, which passes through near the middle of the brain, the two masses of large ganglion cells of the median-eye lobes have coalesced, while the cerebral ganglia are now larger, and the central and cortical groups of large ganglion cells are larger than in Fig. 8. In the third section succeeding large ganglion cells appear on the left side. In Pl. XIII, Fig. 10, the cortical groups of large ganglion cells disappear, and those of the central groups become more numerous. This section involves the origin of the œsophageal ring, and now the posterior end of the brain becomes flatter, wider, and not so deep. Pl. XIII, Fig. 12, represents the posterior portion of the cerebral lobe, with the thick cerebral commissures. In the second section still farther back the ganglion of the first pair of appendages, Pl. XIII, Fig. 13, is intersected, and in Pl. XIV, Fig. 17, the knife passes through the œsophageal ring just behind the ganglia of the first pair of appendages.

In the transverse sections of the brain of a small Limulus, about 2 inches long exclusive of the caudal spine, the details brought out, in addition to those already pointed out, are the very distinct basal portions of the white fibrous portion of the cerebral lobes. These are seen in Pl. XIV, Fig. 18, to send an irregular branch on each side of the median line of the brain (*m*) up to the top of the brain, each branch sending three irregular lobes out to the side of the brain, besides a number of smaller ones which are seen to be cut across, and enveloped by the thick sheets or cylinders of small ganglionic or chromatic cells. (These branches of the cerebral lobes are what Viallanes regards as the stalk of the mushroom or pedunculated bodies). In Fig. 18 the median fissure or space (*m*) between the sausage-like groups of chromatic cells is seen more distinctly than in the fully grown individuals. In this section also the central groups of large ganglion cells (*clgc*) are seen above the cerebral commissure (*c. com*), and are also arranged one group on each side of the median line of the brain.

Pl. XV, Fig. 20, represents a section through the hindermost portion of the brain, the section also passing through the ganglia of the first pair of appendages. It will also be seen here, as in Pl. VI, that the pair of ganglia of the first pair of appendages are quite distinct from the brain, the nerves to these appendages (*1st app. n.*) arising from the mass of large ganglion cells forming a part of the œsophageal ring.

VIII. Results compared with those of other observers.

As may be seen from the preceding descriptions and by reference to the plates, the results of our examination of the brain of the adult Limulus, made with every possible care and pains, and based on many hundred sections, cut not only in a horizontal, but also longitudinal and transverse direction, are the following: The brain of this merostome is composed of but three pairs of lobes,

i. e., two pairs of eye-lobes or ganglia, viz.—first, those which send nerves to the lateral eyes; second, those which innervate the median eyes; and, third, the cerebral ganglia, which, with the mushroom bodies, form the chief portion of the brain. We have seen that the ganglia of the first pair of appendages are separate from the prestomial or prœsophageal brain mass. Hence we throwout these ganglia in our consideration of the constituents of the brain proper.

Prof. Patton, though he has not published any observations on the structure of the brain of the adult Limulus, in his article on the "Origin of Vertebrates from Arachnids" briefly describes (pp. 336–346) the development of the "cephalic lobes" and of the eyes of the embryo of Limulus. Patton does not give details of the structure of the brain of the embryo, only stating such facts as have a bearing on his remarkable theoretical conclusions,* reserving a full description for a future paper. On pages 338 and 339, however, he gives "diagrams" and a "semidiagrammatic" view of the brain of the embryo Limulus and refers to two pairs of median eyes, with their neuromeres, and on page 343 gives a figure of the "fore and mid brain of young larva of Limulus (just hatched) seen from neural surface," in which four preœsophageal neuromeres with their nerves are represented. Deferring to a few pages further on in this essay, the consideration of the number of brain neuromeres in the embryo and larva of Limulus, we will simply remark that we have, after repeated examinations, been unable to find more than a single pair of median eyes† in the embryo or larval Limulus, nor have we been able to detect more than three pairs of neuromeres in front of those innervating the first pair of appendages, these three pairs of neuromeres finally constituting the brain.

Our studies as regards the median-eye lobes entirely confirm those published by Kishinyoue, in his excellent work on the development of the Japanese *Limulus longispina*. He remarks:

> About two weeks before the hatching of the embryo the brain proper becomes divided into two transverse portions by a constriction (Fig. 69). Thus the brain of *Limulus* may be divided into four parts—the ganglion of the median eyes, the ganglion of the lateral eyes, and the anterior and posterior portions of the brain proper.

These last two portions form apparently the cerebral lobes and mushroom bodies. Mr. Kishinyoue has also written me, since his paper was published, that he had only observed a single pair of median eyes.

The only other author besides myself who has studied the brain of the adult Limulus is M. Viallanes. An abstract of his paper read before the French Academy, December 1, 1890, appeared in the Journal of the Royal Microscopical Society, for February, 1891.

The author considers that the brain in *Limulus polyphemus* (this being the species investigated by him) "gives origin to the ocellar nerve," to the nerve of the compound eye, to the cheliceral nerve, to the stomatogastric nerve." We copy his description of the brain:

> *Structure du cerveau.*—Le cerveau se compose de deux paires de centres ganglionnaires. La première est essentiellement constituée comme le *protocérébron* des autres arthropodes et doit être désignée sous ce nom. Quant à la seconde, quelques doutes pouvant encore subsister sur ses homologies, je la désignerai provisoirement sous le nom de *cerveau postérieur*.
>
> *Protocérébron.*—Il se compose d'une paire de nodules fibreux ou lobes protocérébraux relativement petite, réunis sur la ligne médiane par une commissure *préœsophagienne*. Les lobes protocérébraux sont partiellement revêtus d'une écorce de grandes cellules unipolaires; et chacun d'eux donne naissanc eau nerf de l'ocelle correspondant.
>
> Quant au nerf de l'œil composé, il s'unit au lobe protocérébral correspondant, non pas directement, mais par l'intermédiaire d'une formation comparable dans ses traits essentiels au lobe optique des insectes et des crustacés, car on y reconnait les homologues de la lame ganglionnaire, du chiasma externe, des masses médullaires externe et interne; mais chez le Limule ce lobe optique est tres petit relativement et enfoui au sein de la masse du cerveau, au lieu d'être écarté de celui-ci et en contact immédiat avec l'œil composé. Chez le Limule, le nerf optique est donc constitué par des fibres postrétiniennes étirées à l'extrême.
>
> A chacun des lobes protocérébraux est annexé un organe qui, en raison de ses rapports anatomiques et de sa structure histologique, doit être assimilé au *corps pédonculé* des insectes.

---

* With Patton's attempt to derive the vertebrates from forms comparatively high, so specialized and modified as the scorpions and spiders, to say nothing of Limulus, we have little sympathy, regarding them not only as unsound, but as tending to lead to inaccurate observations. On general grounds the attempt to derive the vertebrates from any but the most primitive and generalized vermian forms would seem to be hazardous, the Arthropoda being a specialized and completed branch of the animal series.

† Patton considers that a diverticulum of the median eyebulb "represents, in all probability, a pair of eyes belonging to the first brain segment," and in the next paragraph refers to "the three fused ocelli of Limulus" (p. 344).

As we have already stated M. Viallanes' classification of the regions of the Crustacean and insect brain into three regions, viz, proto, deuto, and tritocerebrum, does not apply to that of Limulus. In my preminminary paper I pointed out that no deutocerebrum or tritocerebrum is represented in the brain of Limulus, and it is to be observed that Viallanes regards the brain as composed of two pairs of ganglia, the first being the protocerebrum, while as to the second he is doubtful, and provisionally calls it the "cerveau postérieur." Viallanes "protocerebrum" is what we regard as the brain proper, and consists originally of three pairs of neuromeres, becoming respectively the ocellar or median-eye ganglia, the lateral-eye ganglia, and the cerebral ganglia.

What Viallanes regards as the posterior brain, and as to the homologies of which he expresses himself as in doubt, we regard as a part of the oesophageal ring, and as postcerebral. This posterior brain gives rise to the cheliceral nerves. The "Commissure transverse pre-oesophagienne" I have detected since Viallanes has called attention to it.

Throwing out then, Viallanes *cerveau postérieur*,* as not forming a part of the genuine brain of Limulus, we will return to the brain proper, or prestomial mass, viz, the protocerebrum of Viallanes.

IX.—THE HOMOLOGIES OF THE SO-CALLED "NUCLEOGENOUS" OR "PEDUNCULATED BODIES."

M. Viallanes describes at some length the structure of the series of plates which we originally† called collectively the "nucleogenous bodies," and the nature and homologies of which seemed to us problematical. He remarks: "To each of the protocerebral lobes is annexed an organ which, by reason of its anatomical relations and its histological structure, should be assimilated to the pedunculated body of insects. The pedunculated body of Limulus has an arborescent form. The lower extremity of its stalk penetrates into the corresponding protocerebral lobe, its upper extremity is divided dichotomously into a great number of branches. These last, which end in truncated extremities, are entirely covered by a thick cortex of small cells very deficient in protoplasm, very deeply colored by stains, emitting very fine fibrillæ, in a word rigorously similar to the elements which form the cellular vestiture of the pedunculated body of insects."

The pedunculated body attains in the Limulus an extraordinary development greater than any other Arthropod known, because it by itself alone forms certainly at least $\frac{33}{1000}$ of the total mass of the brain. This fact is all the more remarkable since up to the present time and not without important reason it has been agreed to consider the development of the pedunculated body as correlated to that of the mental faculties (pp. 2–3).

For years the true relations of these masses or plates which I have called the "nucleogenous bodies" have been a great puzzle to me; they are so numerous and form so large a proportion of the brain; but after an examination of the figures in Viallanes final work I am led to accept his interpetation of these bodies, which he appears to regard as "annexed" to the cerebral lobes. A re-examination of my sections and of my figures, which, however, do not show so clearly as his Pl. x, Fig. 18, the entire stalk of the body, or its intimate connection at its base with the cerebral lobes, leads me to adopt Viallanes view. At the same time there is a remarkable difference observable between these mushroom or pedunculated bodies and those of insects and spiders, a difference to which Viallanes does not refer. This stalk, however, is in part seen in the sections represented by my Pl. xiv, Fig. 18, *st. m. b.*, where the stalk is seen to arise from the bulbous or lateral portion of the cerebral lobes (*b. c. l.*), and to send off an ascending branch, and lateral branches. In Pl. xxxiv, the artotype from a microphotograph of the same section faintly represents the cerebral lobes, and the stalk of the mushroom body arising from the lateral or bulbous portion.

We will first (1) consider their resemblance to the mushroom or pedunculated bodies of insects; (2) their resemblance to or lack of resemblance or homology with the stratified body of the Arachnid brain; (3) their absence, *i. e.*, the unbranched and simple condition of the paired cerebral lobes or ganglia in the freshly hatched Limulus larva.

The mushroom bodies of Dujardin; the two mushroom bodies, with their stems, of Newton, or the pedunculated bodies of Viallanes, and which I have, after Dujardin, called collectively the

* In his last paper Viallanes regards this as the deutocerebrum.

† Farther studies on the brain of *Limulus polyphemus*. Zool. Anzeiger, 20 April, 1891. That the cheliceral nerves are correctly named is doubtful. The so-called chelicera or first pair of appendages of Limulus may be found to correspond to the antennæ or first pair of appendages of the spider discovered by Jarowosky.

mushroom bodies, form a characteristic portion of the brain of adult insects. They have not yet been found to be present in the Synaptera, but occur in the larvæ, at least of those of most metamorphic insects (Lepidoptera and Hymenoptera), though not yet found in the larvæ of Diptera.

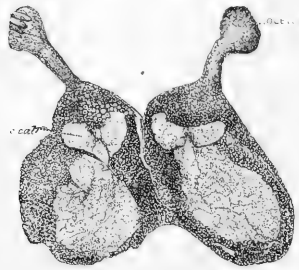

FIG. VI.—Section through the brain of *Caloptenus bivittatus* in the third larval stage, showing the two hemispheres or sides of the brain and the ocelli and ocellar nerves, which are seen to arise from the top of the hemispheres directly over the calices; *o. cal.*, outer calyx of left mushroom body. The lighter portions represent the granulo-fibrous central part of the brain, and the dark the cortical ganglionic cells.

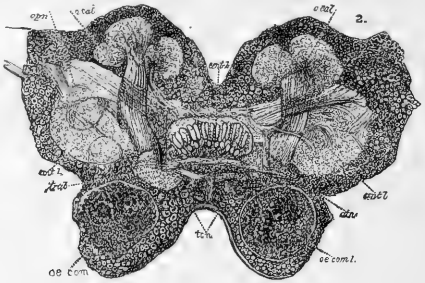

FIG. VII.—Section through the brain of adult *Caloptenus spretus*, passing through the mushroom bodies; *o. cal.*, outer calyx; *centr. b.*, central body; *ant. l.*, antennæ lobe; *op. n.*, optic nerve; *œ, com. l.*, cerebral lobe.

I have found these bodies in the nymphs of the locust (*Caloptenus spretus*), but not in the embryo just before hatching. They occur in the third larval or nymph stage of this insect, and in my essay I stated: "It is evident that by the end of the first larval stage the brain attains the development seen in the third larval state of the two-banded species" (*C. bivittatus*).

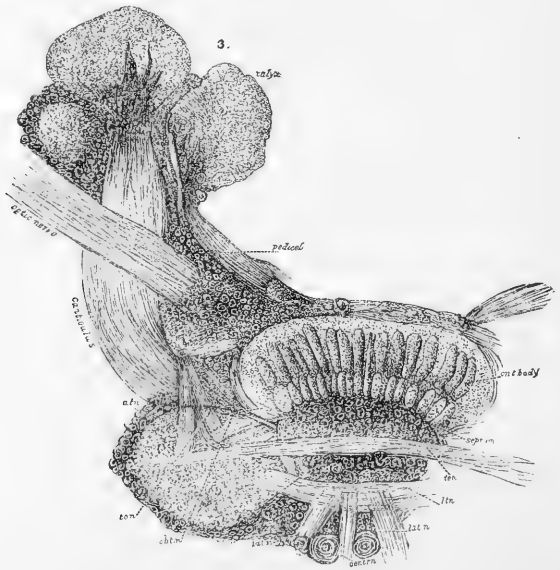

FIG. VIII.—Enlarged view of the trabecula and its nerves, of the mushroom body, its calices and double stalk (*cauliculus and pedicel*), and the origin of the optic nerve.

The result of my studies on the brain of the embryo locust was that from the "embryonic cerebral lobes are eventually developed the central body and the two mushroom bodies" (p. 237). Fig VI, copied from my essay (Pl. XII, Fig. 1), shows the early condition of the mushroom bodies

and their undoubted origin from the cerebral ganglia. Hence these bodies appear to be differentiations of the cerebral ganglia or lobes, having no connection either with the optic or with the antennal lobes. These bodies have, as stated in my essay, attracted a good deal of attention from writers on the brains of insects.

Dujardin, in 1850, first drew attention to them. His memoir we have not at hand to refer to, but as stated by Newton—*

"Dujardin pointed out that in some insects there were to be seen upon the upper part of the brain certain convoluted portions which he compared to the convolutions of the mammalian brain, and, inasmuch as they seemed to be more developed in those insects which are remarkable for their intelligence, such as ants, bees, wasps, etc., he

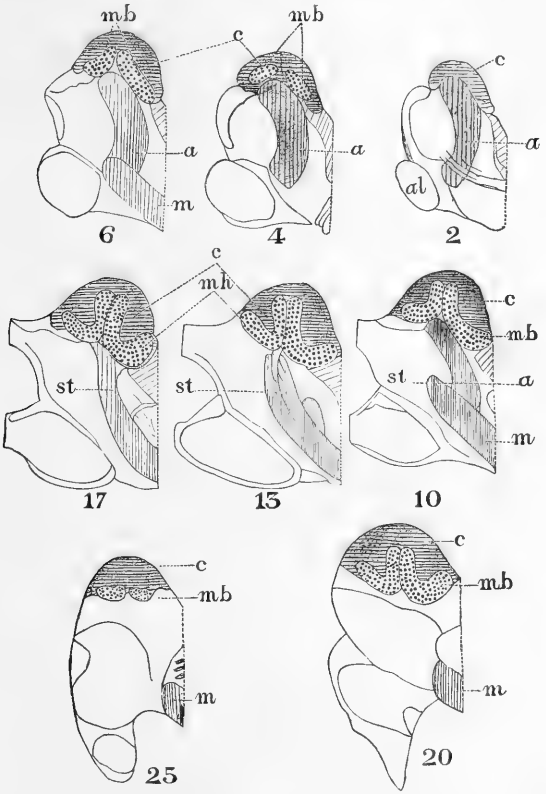

FIG. IX.—Diagrammatic outlines of sections of the upper part of the brain of a cockroach. Only one side of the brain is here represented. The numbers indicate the position in the series of 34 sections into which this brain was cut. *Mb*, mushroom bodies with their cellular covering; *c*, and their stems (*st*); *a*, anterior nervous mass; *m*, median nervous mass.—After Newton.

seemed to think the intelligence of insects stood in direct relationship to the development of these bodies. The form of these structures is described by the same author as being, when fully developed, as in the bee, like a pair of disks upon each side, each disk being folded together and bent downward before and behind, its border being thickened and the inner portion radiated. By very careful dissection he found these bodies to be connected on each side with a short pedicle, which bifurcates below to end in two tubercles. One of these tubercles is directed toward the middle line, and approaches but does not touch the corresponding process of the opposite side. The second tubercle is directed forward, and is in close relation to the front wall of the head, being only covered by the

* On the Brain of the Cockroach. By E. T. Newton. Quart. Journ. Microscopical Science, July, 1879, H, pp. 341, 342.

pia mater [neurilemma]. These convoluted bodies and the stalks upon which they are mounted are compared by Dujardin to certain kinds of mushrooms, and this idea has been retained by more recent writers on the subject."

The form of the mushroom body is much more complicated in the bee or ant than in insects of other orders. In the cockroach and in other Orthoptera, notably the locust, the four divisions of the calices are united into two, while the structure of the calyx in the cockroach is quite different from that of the locust. Mr. Newton, in his description, notwithstanding Dujardin's statement, appears to practically limit the term "mushroom body" to the cap or calyx on the end of the stalk. In the following description we apply the term "mushroom body" to the entire structure, including the base or trabecula, the double stalk, and the cap or calyx. (Pp. 231, 232.)

It may be seen by reference to my figures and those copied from Newton (Fig. IX) and from Viallanes (Figs. X, XI), that the mushroom bodies, though arising from about the middle and lower third of the brain, are mainly contained in the upper region of the brain, this being the position

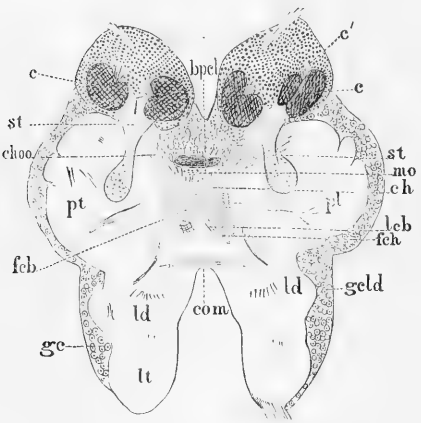

FIG. X.—Transverse section through the brain of the locust (Œdipoda and Caloptenus): *c'*, lower part of *c*, calyx, of mushroom body; *st*, stalk of the same; *b*, *pcl*, bridge of the protocerebral lobes; *mo*, nerve of median ocellus; *ch*, transverse fascia of the optico-olfactory chiasma; *feb*, fibrous region of the central body; *tcb*, tubercle of the central body; *fch*, descending fascia of the optico-olfactory chiasma; *choo*, superior fascia of the optico-olfactory chiasma; *pt*, *pl*, protocerebral lobes; *ld*, dorsal lobe of the deuto-cerebrum; *lt*, trito-cerebral lobe; *geld*, *gc*, ganglion cells.—After Viallanes.

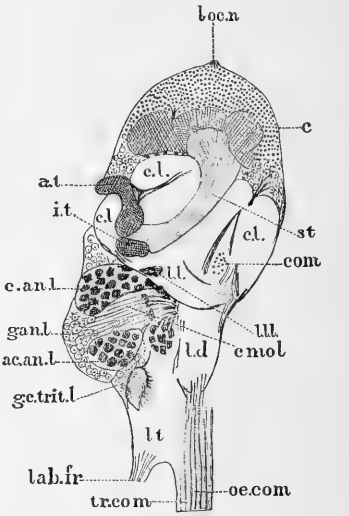

FIG. XI.—Sagittal section through the brain of the locust: *l. oc. n*, lateral ocellus nerve; *at*, anterior tubercle of the pedunculated body; *it*, internal tubercle of the pedunculated body; *cl*, cerebral lobes; *ll*, lateral lobe of the middle protocerebron; *com*, commissural cord; *c. an. l.*, cortical layer of the olfactory lobe; *cmol*, central mass of the olfactory lobe; *ac. an. l*, fibers uniting the median lobe of the middle protocerebron with dorsal lobes of the deutocerebron; *gc.*, *trit*, *l*, ganglionated cortex of the trito-cerebral lobe; *g an. l*, cortex of antennal (olfactory) lobe; *lab. fr*, labro-frontal nerve; *oe. com*, œsophageal commissure; *tr. com*, transverse commissure of œsophageal ring; other letters as in Fig. X.—After Viallanes.

of the caps of the mushroom, or calyces, these in part, as in the figures of Viallanes, forming two lobe-like protuberances (*c*, *c'*), the base of the stalk scarcely reaching the middle of the brain; in fact, being confined to the upper third of the brain. But in Limulus the masses of aprotoplasmic cells, with the fibrillæ arising from them, constitute nearly the lower half of the entire brain, besides forming a thick cortical envelope on the sides and in front and behind, and constituting, as M. Viallanes himself declares, $\frac{99}{100}$ of the whole brain*. I was led, therefore, to think that these structures were not the homologues of the mushroom bodies of insects, but rather the cortical portion of the cerebral ganglia, with its lobules, besides forming a part of the cortex of the optic lobes; all the fibrous or fibrillar portion of the brain being in part derived from what we have variously called the chromatic or aprotoplasmic, or small ganglion cells, and in part from what we call the

* This is somewhat of an exaggeration, and $\frac{80}{100}$ would seem to be nearer the correct proportion.

large ganglion, viz, the normal ganglion cells, in which the nucleus is surrounded by an abundant protoplasm.

It should also be observed that the mushroom bodies are best developed in adult insects, and especially in those of a high degree of intelligence. Now Limulus is low in the plane of intelligence. It burrows in the mud and in a haphazard way devours whatever worms and other soft-bodied animals it can obtain with its spiny-based legs.

On the other hand we were, before reading Viallane's final memoir, inclined to homologize the "nucleogenus bodies" of Limulus in part with the cortical masses of chromatic cells figured by Saint Remy (Figs. XII and XIII *l. ol.*) which envelop the optic lobes of spiders and the cerebral lobes of the scorpion (Fig. XIV *a. gang. m.*).

Whether a pedunculated body is present in the brain of myriopods appears from the careful researches of Saint Remy to be a matter of doubt. He does not seem to have detected any organs like them in the genera he investigated except in Julus, where he observed some vestiges which he compares to the pedunculated bodies of insects. In Scutigera (Cermatia) he discovered what he doubtfully homologizes with the pedunculated bodies of insects, remarking as follows:

The homologies of the complicated apparatus that we have just described are difficult—we may even say impossible—to establish with certainty. The general aspect and the disposition of the principal parts leads one at first to think that this ensemble represents the pedunculated body so constant in insects and the vestiges of which we have found in Julus. But when we examine the thing more closely and push the comparison more thoroughly we immediately perceive that the resemblance is absolutely superficial and that we can not find points of precise resemblance between the portions of our apparatus and those of the pedunculated body of insects. We are here even less well informed than in Julus because there are wanting the relations with the optic lobe (commissures of Bellonci) which have served as in this case to affirm the existence of a rudimentary pedunculated body represented by a calyx.

From the lack of facts of this kind it must be acknowledged that we have to content ourselves with hypotheses, though quite plausible ones. Without seeking to compare these organs in their details, we shall regard them as very probably homologues. What are, indeed, the constituent parts of the pedunculated body of insects? An accumulation of chromatic cells in relation with a system of medullary stalks which are planted in the protocerebron, and end abruptly in the midst (*au sein*) of the punctuated substance. We shall find the same structure and the same arrangements in the pedunculated organs of Scutigera. The peduncles end near the median line, as does the beam (trabecula), and the internal tubercle ends near the neurilemma, as the anterior horn in these last. The thin ganglionic masses seem to play, opposite these parts, the same role as the calices opposite (*vis-à-vis*) the horn and the beam (*poutre*) (pp. 74, 75).

In Peripatus also Saint Remy describes and figures a system of plates and a medullary mass perhaps comparable to the pedunculated organ of Scutigera, as he states on p. 242:

Ce système des lames et de la masse médullaire peut être comparé à l'organe pédonculé de la Scutigère. Ici comme chez la Scutigère, nous avons un organe médullaire qui recueille, d'une part, les prolongements de petites cellules chromatiques pauvres en protoplasma, et est en relation, d'outre part, avec des pièces qui s'enfoncent dans la substance ponctuée et se terminent franchement sans contracter de rapports à l'extremité avec d'autres régions. Mais, outre ce rapprochment fondé exclusivement sur des caractères generaux, il est possible d'en faire un autre avec le corps pédonculé des insectes, basé sur les mêmes caractères et appuyé de plus sur un fait anatomique interressant, l'existence de relations entre ces organs et le lobe olfactif, ainsi que la région qui donne naissance au pédicule optique, disposition commune à l'organe que nous venons d'etudier chez le Péripate et au corps pédonculé des insectes.

Under the circumstances, then, we were at first unable to agree with M. Viallanes that what he regards as pedunculated bodies are really such, nor did they appear to be the homologues of the problematical organs in the brain of Onychophora (Peripatus), or of Myriopoda. Further and very extended examination of the brain of young Limuli after their first molt, and when they are less than an inch long, exclusive of the caudal spine, are urgently needed to finally settle this and other difficult points in the homologies of the brain of Limulus.

X. COMPARISON OF THE BRAIN OF LIMULUS WITH THAT OF ARACHNIDA.

Thanks to the able and very detailed account and beautiful figures of Dr. Saint Remy, we now have a means or standard of comparison in studying the brain of Limulus which has not hitherto been afforded us, and which have greatly aided us in coming to a better appreciation of the nature of the brain of Limulus. There seems little doubt but that the brain in question is in its general features much like that of Arachnida. This is largely owing to the similarity in the

shape and position of the optic ganglia or lobes, and the similar relations in the mode of origin of the optic nerves; both the Arachnida and Merostomata having median and lateral eyes with a, in general, similar position in respect to the exterior of the head. Besides this, neither class possesses optic ganglia closely resembling those of insects and Decapod crustacea.

And yet there is a noteworthy difference between the brain of Limulus and of Arachnida. In the latter the cerebral ganglia are large and well developed, forming, we should roughly estimate, two-thirds to three-fourths of the brain. The central medullary or white fibrous portion is largely developed, forming the bulk of the cerebral ganglia, and is more or less spherical in shape, while the cortical layers or masses of large ganglion cells are large and thick, the cells themselves being abundant, whereas in Limulus they are scanty, forming isolated small groups. Reference to the accompanying figures, copied from Saint Remy's work, will show the structure of the Arachnid brain together with the resemblance to and the difference from that of Limulus.

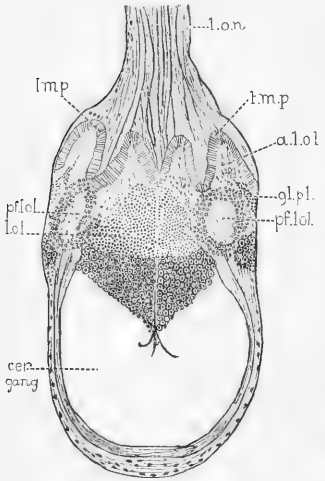

FIG. XII.—Brain of *Lycosa narbonensis* Walck., horizontal section passing through the middle of the middle segment of the optic lobes and through the lower medullary plate, and through the middle part of the lower medullary mass. *l. o. n.*, lower optic nerve; *l. m. p.*, lower medullary plate; *a. l. ol.*, anterior fibrillar layer of the lower optic lobes; *gl. pl.*, glomerulated plate of the lower optic lobule; *pf. lol.*, posterior fibrillar layer of the lower optic lobule; *l. o. l.*, lower optic lobe; *cer. gang.*, cerebral ganglion.—After Saint Remy.

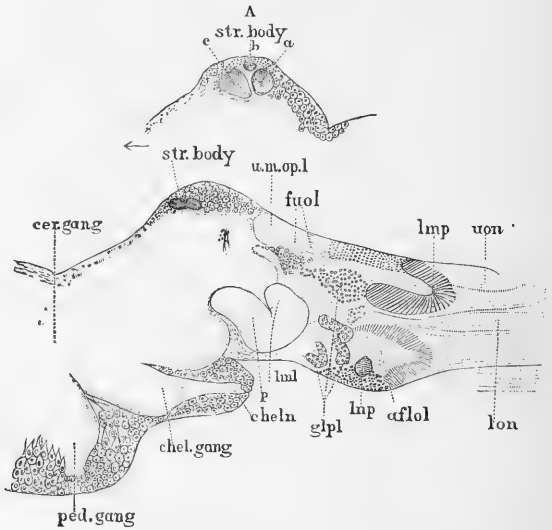

FIG. XIII.—Longitudinal (sagittal) section of the same, passing through a plane situated near the junction of the outer third with the middle third of the brain. *str. body*, stratified body; *u. m. o p. l.*, upper medullary mass of the upper optic lobe; *f. u. o. l.*, fibrillar layer of the upper optic lobule; *u. o. n.*, upper optic nerve; *l. o. n.*, lower optic nerve; *l. m. p.*, lower segment of the lower medullary plate; *l. m. l.*, lower medullary mass of the lower optic lobe; *p*, head of the lower medullary mass; *chel. n.*, cheliceral nerve; *chel. gang.*, cheliceral ganglion; *ped. gang.*, ganglion of the pedipalp.—After Saint Remy.

A. Part of a transverse section through a plane near the middle of the brain, to show the stratified body (*str. body*). *a*, principal plate of the anterior segment of the stratified body; *b*, accessory plate of *a*; *c.*, posterior segment of the stratified body.—After Saint Remy.

I have been unable to detect any trace in the brain of Limulus of the posterior stratified body (Fig. XII–XIV, *str. body*) which is regarded by Saint Remy as the homologue of the "pedunculated body" of insects. Neither does M. Viallanes refer to any organ similar to that discovered by Saint Remy.*

The position of this organ and its structure should be noticed. Both in spiders and the scorpion it has nearly the same situation as in insects, being placed in the uppermost region of the head in a lobe-like swelling projecting above the general surface of the brain. In the side view of the scorpion's brain (Fig. XIV *str. body*) it is seen to be somewhat trilobate and divided into an

* But in his final paper, p. 449, he very briefly states that this organ, "although modified, is likewise recognizable in the Arachnids, where it has been described by M. Saint Remy under the name of *organe stratifié*."

upper and lower portion, but without any stalk passing downward into the central portion of the brain.

Dr. Saint Remy describes this body at length under the name *organe stratifié postérieur*, and says that it is situated on the very salient posterior and upper border of the brain, forming a prominent projection above the punctuated mass of the cerebral lobes. It comprises a principal medullary portion and a cellular covering. It is formed of parallel alternate clear and obscure bands.

That this organ is apparently not homologous with the mushroom bodies of insects appears to be proved by the fact that it is single, not a paired organ.

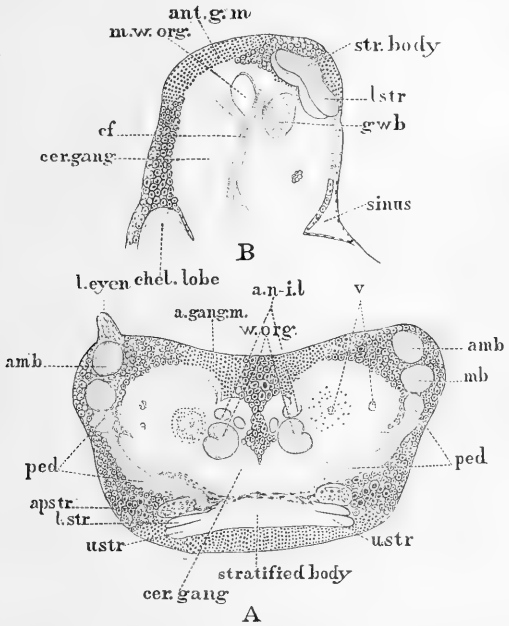

FIG. XIV.—A, horizontal section passing through the upper part of the brain of the scorpion (*Buthus occitanus* Amorx.) through the lower optic lobe or ganglion. *cer. gang.*, cerebral ganglion; *l. eye n.*, lower eye nerve; *amb*, anterior medullary ball of the lower optic ganglion; *m. b.*, middle medullary ball of the same; *ped.*, common peduncle of the optic lobules; parts of the stratified organ or body; *l. str.*, lower segment; *u. str.*, upper segment; *apstr*, anterior plate (lame) of the upper segment of the same; *a. gang. m.*, anterior ganglion-mass; *an. i. l.*, antero-internal lobule; *w. org*, principal medullary mass of the anterior segment of the wallet-shaped organ; *v*, vessel (artery); *B*, longitudinal (sagittal) section of the same passing through the union of the internal third with the middle third of the brain. Very young individual, × 53 diams., *g. w. b.*, principal glomerulated mass of the posterior segment of the wallet-shaped organ; principal medullary mass of the anterior segment of the wallet-shaped organ; *ant. g. m.*, anterior ganglion mass; *chel. lobe*, ganglion innervating the first pair of appendages; *c. f.*, commissural fascia.—After Saint Remy.

In the scorpion (Fig. XIV, *str. body*) the stratified body differs somewhat from that of spiders, but is essentially the same. "But the most interesting feature about it," says Saint Remy, "is the relation which exists between this organ and the optic lobe by the medium of the common peduncle." Although the stratified body of Arachnida is described and figured as unpaired, yet in deference to the opinion of Saint Remy I provisionally accept his view that it is the homologue of the pair of pedunculated bodies of insects. I may add that it is a matter of surprise to me that M. Viallanes does not dwell more on the remarkable differences between the brains of Limulus and of the Arachnida, particularly the great differences between the mushroom-bodies of Limulus and their homologues in Arachnida, since he adopts the opinion that Limulus is an Arachnidan. On the other hand these striking differences in the morphology of the brain tends to my mind to furnish additional proof that Limulus is the representative of a different class of Arthropods.

Another organ which is characteristic of the scorpion's brain we have failed to detect in that of Limulus, nor does Viallanes mention it. Saint Remy thus describes that of the scorpion:

The structure which, for want of a better name, we shall designate under the name of *wallet-shaped organ* (*organe en bissac*) to recall its general form, occupies the internal and middle part of the cerebral lobe. It comprises two segments united by a much smaller middle portion in the form of a neck (p. 224).

Still another organ also present in the scorpion's brain which we have not found in the brain of Limulus, and which is not mentioned by Viallanes, is the *olivary body.* It is situated in the posterior region of the cerebral lobe below the wallet-like organ near the median line; it is an olive-shaped mass of dense punctured substance and situated obliquely.

Considering, then, the fact that the deutocerebrum or its homologue is in Limulus separate from, where in Arachnida it is fused with the brain; also the differences in the shape of the cerebral lobes, the immense development of the ruffle-like plates or masses of small chromatic ganglion cells forming the pedunculated or mushroom bodies; the small number of large ganglion cells; the absence of the wallet-shaped and of the olivary organs found in the brain of scorpions, and

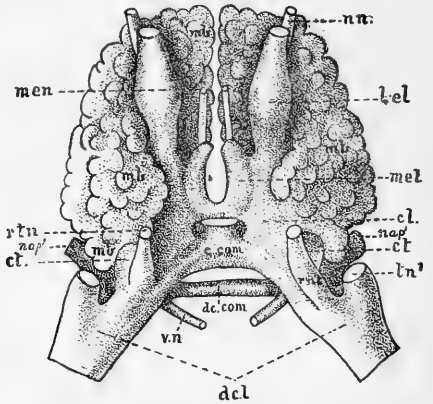

Fig. XV.—Brain of *Limulus polyphemus*, drawn by Viallanes, from a model in relief of the brain of Limulus, made of wax, seen from the dorsal aspect, the neurilemma having been removed. *l. e. l.*, lateral-eye lobe; *m. e. l.*, median-eye lobe; *m. e. n.*, median-eye nerve; *n. n.*, nerve passing to the neuropore of Patten (*fossette sensitive* Viallanes); *m. b.*, *m. b.*, *m. b.*, *m. b.*, lobules of the mushroom or pedunculated body; *c. t.*, cerebral tubercle in part, giving rise to the stalk of the mushroom body; *c. l.*, cerebral lobes; *r. t. n.* and *r n. t.*, recurrent tegumental nerve; *n. a. p.*, nerve of first pair of appendages (cheliceral nerve of Viallanes); *c. com.*, cerebral commissure; *d. c. com.*, deutocerebral commissure; *d. c. l.*, deutocerebral lobes; *v. n.*, root of visceral or sympathetic nervous system.—After Viallanes.

It is to be observed that the median-eye ganglia are not correctly represented by the model, the horseshoe shaped mass simply representing the fibres. See my Pl. VII, Fig. 1. This empty median oval space is, in nature, filled with large and small ganglia cells, and the roots of the fibres originating from them.

the absence of the peculiar medullary plates present in the optic lobes of spiders, we see that while the brain of Limulus is in most respects simpler, it also presents noteworthy differences from that of the Arachnida.*

* Since this paper was put in type, and a few days before obtaining the proof, I received the Annales des Sciences Naturelles, Zoologie, Nos. 4, 5, 6 for March 10, 1893, containing M. Viallanes' final paper on the brain of Limulus.

The account of the internal structure of the brain is brief, occupying but five pages, and ends with an "*Aperçu général de l'organisation du système nerveux des Articulés.*" The article is illustrated with two folding plates. Only two actual sections of the brain of Limulus are represented. One (Pl. 10, Fig. 17) represents a horizontal section passing through the lateral-eye ganglion ("ganglion optique") of one side, and the other (Fig. 18) of a horizontal section lower down passing through the stalk of the pedunculated body.

This last figure clearly shows what my sections has failed to do, except partially, the well-defined stalk of the mushroom, or pedunculated body, and shows that what in the first place I had described as the "nucleogenous bodies," are lobules or branches of a pair of organs probably homologous with those of insects. This leads me to accept M. Viallanes' view of the homology of these extraordinarily developed organs with the two mushroom bodies of insects. In accordance with this view I have corrected the text of the present article. Viallanes has also pointed out and drawn the chiasma of the median eye, structures which I had failed to see; and he shows that the the basal

XI. Notes on the embryonic development of the brain and ventral cord. Plates XVIII and XIX.

The general morphology of the brain of Limulus can not be with certainty fully worked out without a knowledge of the embryology of the nervous system, especially of the relations of the neuromeres of the head and of the changes which take place in the relative arrangement of these neuromeres, and of the lobes formed by them during the development of the parts of the head in the later embryonic stages.

Also, the mode of development of the ruffle-like masses of chromatic or aprotoplasmic ganglion cells will have to be studied during the period of larval life succeeding the first molt, and before the body becomes, say, about an inch in length without the caudal spine. With the results of Prof. Patten's work we are not satisfied, as we feel by no means sure that his diagrams in his Figs. 7, 8, 9, and 10, however ingenious, are in all respects reliable, and are confident that no more than a single pair of median eyes actually exist in nature. We have found no traces of a second pair of median eyes, nor has Kishinouye detected them. Until, then, Prof. Patten publishes his observations in full we should prefer to wait before entirely accepting his diagrammatic figures and some of the views expressed in his paper.

The most important observation on the development of the brain of Limulus are those of Mr. Kishinouye, who seems to have paid special attention to this subject. He states:

> The lateral halves of the nervous system develop independently of each other. Each half of the brain with its corresponding ventral nerve cord is produced as a continuous long cord of epiblastic thickening just inside the base of the appendages (Figs. 12-14). It is easy, however, to distinguish the brain from the ventral nerve cord. When they are first formed, the former is very much broader than the latter, occupying almost the whole of the segment of the cephalic lobe, while the ventral nerve cord occupies only about one-third of the breadth of each appendage-bearing segment (Fig. 12).

Kishinouye then describes the "paired small invagination" which appears in the lateral part or margin of the brain, and another paired epiblastic invagination along the anterior internal corner of the margin of the brain. These cephalic invaginations are, however, very shallow, and disappear before the separation of the nervous system from the epiblast takes place.

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portions of these lobes belong to the lobes in question. I had regarded them as lateral lobules of the cerebral lobes, but now accept Viallanes' view as to their nature.

M. Viallanes has also succeeded better than myself in making a wax model of the interior structure of the brain, giving a dorsal, ventral, and a sagittal view, and I reproduce his figure of the model of the dorsal view as it shows better than I could do the relation of the optic and ocellar lobes to the cerebral lobes. I am able to confirm the accuracy of his work, and am glad to bear tribute to the skill and patience he has shown in working out the structure of the brain of this animal. On pages 449 and 450 he discusses the organization of the brain of Limulus and of Arachnids. He very briefly (in three lines) states his belief that the two pedunculated bodies of Limulus are the homologues of the "striated organ," of Arachnids, but does not enter into details, or attempt to show how the two bodies in Limulus can be homologized with the single stratified organ of Arachnids. Neither does he refer to the very great differences between the size and shape of the cerebral hemispheres of Limulus and Arachnids, and to other differences to which I have drawn attention. I can not agree with M. Viallanes that the brain of Limulus is the exact homologue of the brain of Arachnides; I hold that the "deuto cerebrum" does not form a part of the brain proper, that it is not fused with it, that it is post or at least paracsophogeal, since it innervates the first pair of appendages, and this shows that Limulus is in this respect more primitive than the Arachnids. The fusion of what were originally distinct ganglia (see my Pl. XVIII, Fig. 7) has never gone on so completely as in the Arachnids. Hence the brain characters, together with the absence of the urinary tubes, and of tracheæ, and the presence of branchiæ, besides the shape of the six pairs of cephalic appendages and the large median eyes, as well as other minor characters, are sufficient in importance to make Limulus the representative of a class by itself, with which the trilobites should be associated.

I may be allowed to add that M. Viallanes' contemptuous critique of my first very imperfect account of the brain of Limulus, published in 1880, is a grain harsh and unfair, since before writing it he must have had in his hands my brief abstract of the present paper published in the *Zoologischer Anzeiger* for April 20, 1891, and a copy of which I mailed to him. Even in my first account published in 1880, while I incorrectly stated that the brain was unsymmetrical, I called attention to and figured the "nucleogenous bodies," and pointed out their enormous development. To my discovery of these important structures M. Viallanes condescends to make no reference; I had also pointed out the differences between the large ganglion cells and the small aprotoplasmic ones, or the "nuclei" composing the nucleogeneous bodies. I did not point out clearly the limits of the median and lateral eye lobes, and those of the cerebral lobes, because in my osmic acid preparations (made in 1879) they are not shown so well as in those stained with carmine.

He then adds:

The part of the brain formed by the external groove becomes the optic ganglion of the lateral eyes, as in the case of the spider. The optic ganglion of the median eyes is produced from the epiblastic thickening forming the united mouth of the invagination for the median eyes (Fig. 69, g. med. *e.*, *our* fig.).

The brain, which was almost circular in its outline, as its height was almost equal to its breadth (Figs. 12, 34) becomes afterwards semicircular (Fig. 13), later still sickle-shaped (Fig. 14), and shortly before hatching almost straight (Fig. 69). This is caused probably by the peculiar development of segments. All the segments seem to develop most vigorously at the line midway between the ventral and dorsal median lines, *i. e.*, all the segments have their greatest antero-posterior extension on this line, and become shorter and converge, like the frame pieces of a folding fan, toward both the ventral and dorsal median lines. Therefore the external ends of the brain are pushed anteriorly by the growth of the succeeding segments. About two weeks before the hatching of the embryo the brain proper becomes divided into two transverse portions by a constriction (Fig. 69). Thus the brain of Limulus may be divided into four parts; the ganglion of the median eyes, the ganglion of the lateral eyes, and the anterior and posterior portions of the brain proper. These four parts are arranged in three transverse rows. The anterior row is occupied by the two pairs of the optic ganglia, the middle row by the anterior portion of the brain proper, and the posterior row by the posterior portion of the brain proper (Fig. 69).

We have quoted Kishinouye's observations at length, because they clearly and simply explain as no one had done before, the mode of origin of the ganglia of the brain. In Prof. Kingsley's last article little is said upon this subject, his attention not having apparently been directed to the development of the ganglia of the brain.

My own imperfect observations confirm those of Kishinouye, but were made on a stage apparently before that represented by his Fig. 13, and after that of his Fig. 12. The legs in my embryos had not yet become divided at the ends into claws, while there were three pairs of abdominal appendages. It also appears to be of a later stage than that represented by Kingsley in his Fig. 32, though the ambulatory or cephalothoracic legs of my embryos seem less advanced in development. In my embryos also the neuroblasts had disappeared, though I made repeated attempts to discover them. Kishinouye states that "they disappear when the ventral nerve cord is divided into ganglia and begins to be separated from the epiblast" (p. 73).

Kingsley's Fig. 32 well represents the cerebral and lateral-eye lobes; but his sketch does not give a clear view of the median-eye ganglia, which in my specimens were distinctly separated from the lateral-eye ganglia and the cerebral lobes, and were somewhat conical in shape. I reproduce on Pl. XVII, some camera sketches of the lobes of the brain seen in the stage represented by the shaded Fig. 1, the mouth at this time being situated between the first pair of appendages. The eggs were taken from the vicarious chorion or deutovum, and stained from two to three minutes in alcohol cochineal, so as to bring out quite clearly the ventral plate and parts of the germ, which had been freshly killed. All the figures on this plate were made from a single embryo.

In Fig. 2 the relation of the lobes is shown by a camera sketch made in direct sunlight. The lateral-eye lobes or ganglia are seen to be distinct from the cerebral ganglia (*cer. gang.*), and in front of the former are the triangular median-eye lobes. I could not detect any traces of a second pair of median-eye lobes or median eyes; and, as already stated, I am led to think that Patten was mistaken in supposing that they exist. Just above the mouth (*m*) is a shield-shaped or somewhat triangular convex area, which is not figured by Kingsley, and of the nature of which I am doubtful, unless it be the rostrum or upper lip. It was seen very distinctly and at different times. In front of it is a small depression (probably the neuropore of Patten), and a larger one is seen in front of the union of the cerebral lobes.

Fig. 3 is another sketch made from the same egg, showing the same parts from a side view. In this figure there is represented an irregular depression between the second pair of abdominal appendages, which, however, was not always seen. Fig. 3*a* is a camera sketch of the head of the embryo seen from one side, the left side being the part most distinctly seen.

The neuromeres were distinctly developed, a pair to each pair of appendages. In the abdomen three pairs were distinctly seen, as represented in Figs. 4, 5, and 6. I was able to see them very distinctly at different times. In Kingsley's Fig. 32 no abdominal neuromeres are represented. His figure may represent a later stage, though I hardly understand why he does not represent the third pair of abdominal legs, which I repeatedly saw, my Fig. 5 being a careful sketch of those of the right side made in direct sunlight. In Fig. 6 the vent or proctodæum was observed, situated between the last two neuromeres.

Thus far our results tend to prove that there are in the embryo three pairs of prestomial brain ganglia: (1) the median-eye ganglia, (2) the lateral-eye ganglia, and (3) the central or cerebral ganglia with their outgrowth, the mushroom bodies. We have been able to detect these in the brain of the adult Limulus, and have been unable to find any other important fundamental structures in the brain proper.

The changes which the different lobes of the brain undergo in late embryonic and in early larval life have in part been described by Dr. Patten, and briefly by Kishinouye, but need further elucidation. The problem is a difficult one, and we need material for it, which no observer has yet apparently had, viz, specimens after the first molt. In the trilobite stage, as seen in Kishinouye's Fig. 45, reproduced on this page, the medulla or central white fibrous portion (*f*) is differentiated from the ganglionic cortex (*g c*), but his figure does not include the optic ganglia.

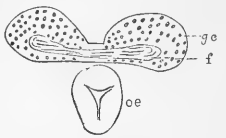

FIG. XVI.—The brain of Limulus in the trilobite stage.—After Kishinouye.

Pls. XVIII and XIX represent sections of the brain of the larva. So far as I have been able to make out from my sections, the cerebral ganglia grow rapidly in size, the median-eye lobes sink in below the level of the upper side, the lateral-eye ganglia overlying them and forming the two lateral superior swellings of the upper surface of the brain. The median-eye lobes are partly coalesced, and the nerves proceeding from them grow together on leaving the brain, only separating at the median eyes. At this period the mushroom bodies have not yet been developed.

XII. Observations on the development of the abdominal appendages, and of the gill-sacs or branchiæ. Plate XX.

The unusual amount of interest attached to Limulus, and the great diversity of opinion which has been, and still is, held by zoölogists in regard to its affinities, seems mainly due to the fact that this animal is a composite or generalized type, with most important features peculiar to itself and to its class; it also has some points of resemblance to the Phyllopod Crustacea, which are perhaps the most generalized and primitive group of Crustacea, unless the Phyllocarida be excepted. On the other hand its embryology and some anatomical characters ally it still more closely with the Arachnida, so much so that it seems, contrary to our earlier views, not unreasonable to suppose that the two groups may have had a common origin; though the Merostomata, with the Trilobites, were with little doubt developed much earlier than the Arachnida, the class Podostomata being nearer their vermian ancestors than the Arachnida.

When we take into account the Cambrian Paradoxides and the Silurian Arethusina with their very numerous (about 30) segments, and what we know from Walcott's researches of the probable nature of the legs of Calymene, Ceraurus, Acidaspis, etc., we can see that the independent evolution of such Trilobites from some branchiate Annelid was quite as natural and probable as the derivation of some Protophyllopod, or Protophyllocaridan Crustacean from a branchiate Annelid worm, and that it probably took place at an earlier geological epoch.

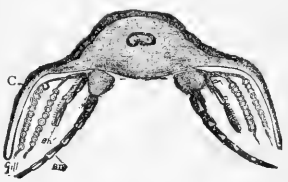

FIG. XVII.—Restored section of the thorax of a Trilobite (Calymene). *c*, carapace; *en*, endopodite; *en'*, exopodite, with the gills on the epipodal or respiratory part of the appendage.—After Walcott.

Examining Walcott's restoration of the underside of *Calymene senaria*,* as well as his figures of actual sections, we notice a great uniformity in all the appendages from the head to the end of the pygidium, which is paralleled by that of the limbs of Phyllopods. True, in the Trilobites there were no functional antennæ and mouth-parts, and all the limbs, both of the head, thoracic region, and of the pygidium, were similar in shape, being cylindrical and short, thus fitted for walking, and bore dorsal branchiæ.

The branchiæ, says Walcott, as found in Calymene, Ceraurus, and Acidaspis have three forms. In the first form they divide a short distance from the attachment to the basal joint of the leg and

* Bulletin Museum Comp. Zoöl., VIII, Pl. VI, Fig. 1, 1881.

extend outward and downward as two simple, slender tubes or ribbon-like filaments. In the second form they divide in the same manner, but the two branches are spirals. (See Fig. XVII.)

The third type, which is apparently confined to the anterior segments of the thorax, is figured in his Pl. III, Fig. 2. Here there was a series of at least 17 thin leaves arranged from above

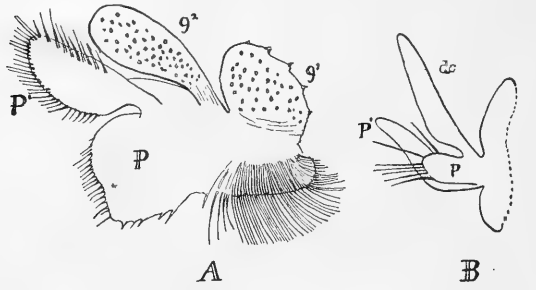

FIG. XVIII.—A, a leg of *Branchinecta lindahli* (from 10th pair); g^1, g^2, gills; P, P^1, the two parapodium-like lobes, comparable with those of the annelid Lyarete (B), *dc*, dorsal cirrus, acting as a gill.

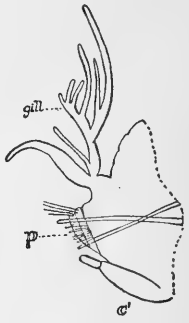

FIG. XIX.—Leg or parapodium of *Eunice conglomerans*, with a branched gill and the ventral cirrus (c^1) divided into two joints.—After Ehlers.

downwards, not spiral but flat, somewhat as in Limulus, and radiating vertically from a jointed epipodite or branchial arm. Thus as in forms like Calymene, Asaphus, Bronteus, etc., all the limbs behind the mouth-region were cylindrical, ambulatory, and branchiferous, but those of the pygidium were not broad and flat and adapted for swimming, as in Limulus. Thus the Trilobites were less differentiated and more closely allied to the Annelid type than the Eurypterida and Limulus. It thus seems probable that the three great groups of Arthropoda had each an independent origin from the higher worms, or from extinct forms like them. The insects, with the Myriopods, were independently evolved from some Chætopod worms of unknown affinities by way of Peripatus; the Podostomata* by an independent path also originated from a true branchiate Annelid, while the Crustacea with little doubt, as generally conceded, arose from some Annelid-like form; perhaps one with dorsal cirri acting as branchiæ, like those of *Lyarete braziliensis*, figured by Ehlers (Mem. M. C. Z., 1887), these being remarkably like those of Branchipus and other Phyllopods.† (Fig. XVIII, B.)

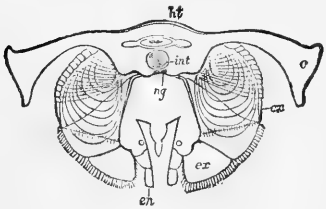

FIG. XX.—Section through the abdomen of Limulus; *c*, carapace; *ht.*, heart; *int.*, intestine; *ng.*, ganglion; *en*, axial jointed endopodite; *ex* epipodal portion bearing the gills.

It is also to be borne in mind that in the trilobites, the branchiæ were dorsal though lying under the dorsal wall of the body, and attached to an epipodal division of the limbs, and so they are in Limulus, as shown by our Fig. XX. This dorsal position of the gill-plates should be taken into account when comparing them with the book-leaves of Arachnids.

* The class Podostomata includes both the Merostomata, of which Limulus is the living representative, and the Trilobites.

† The problem of the derivation of the jointed limbs of Arthropods from the soft non-jointed Annelid parapodium is paralleled by that of the origin of the limbs of the higher vertebrates from the fins of fishes. The limbs of Arthropods are divided into a few or many leverage systems, represented by segments or joints. There are all grades of Arthropod limbs, from the unjointed parapodia-like limbs of Phyllopods, which are most Annelid-like, to the imperfectly jointed swimming legs of the Nauplius of various Crustacea, and to the abdominal legs of Malacostraca, up to the ambulatory legs of Decapods and of terrestrial tracheate Arthropods. These varieties of shape can be explained by adaptation to changed conditions resulting from a change from an aquatic to a terrestrial life, or from simply swimming to walking on the bottom or to burrowing in sand and mud. On the other hand the appendages of Syllid worms are often jointed, and in Eunice (Fig. XIX) and Polynoe, the lower division of the parapodium consists of two joints.

In the Merostomata there must have been a considerable diversity of shape and mode of attachment. Fortunately we know something of the form of those of Slimonia, an Eurypterid. Dr. Henry Woodward has described and figured them in his valuable Monograph of the British Merostomata (Pl. XIX, Figs. 3 and 4, p. 115). Similar ones in *Pterygotus bilobus* have been described and figured by him. (Pl. XII, Fig. 1*d*). Woodward thus describes those of Slimonia:

They appear to be arranged in linear series and were attached in single or double rows to the under surface of the body by their upper end, whilst their lateral and lower rounded leaflike borders were freely bathed in the fluid medium in order to oxygenate the blood.

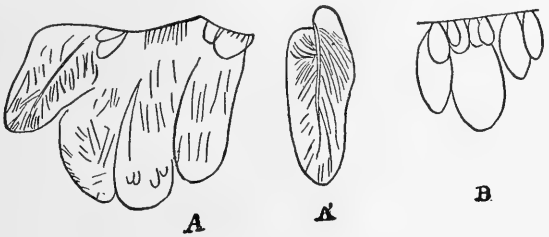

FIG. XXI.—A, gill-leaves of Slimonia; A¹, a separate one showing the "vascular striæ;" B, those of Pterygotus, both large and small. After Woodward.

These leaflike appendages are highly vascular; they are about two inches in length and three-fourths of an inch broad, but they vary in size, having probably been largest near the center of the body, becoming smaller as they approached the sides (p. 115, 116).

These delicate membranous plates in Pterygotus differ in form from the corresponding organs in Limulus; but there is no doubt they occupied the same relative position. In Limulus the vascular striæ are parallel to the circumference of the lamellæ; in Pterygotus they appear to have branched and subdivided from the center to the margin of the plate, becoming finer and more numerous toward the border* (p. 68).

HISTORY OF OPINION AS TO THE HOMOLOGY OF THE GILL-BEARING ABDOMINAL LEGS OF LIMULUS WITH THE BOOK-LUNGS OF ARACHNIDA.

Nothing was said of the mode of origin of the book-lungs of the Arachnida until the appearance of Metschnikoff's Embryologie des Scorpions (1870). He states: "The second pair of abdominal appendages are transformed into the comblike organs, while the appendages of the other segments of the abdomen totally disappear." *In the place of the four pairs of the same* (*not, however, developing from these*) *appear eight gill-pouches* (Kiemenlöcher).

Further on Metschnikoff describes the development of these lungs:

The lungs form invaginations of the chitinous layer which are situated directly under (*dicht unter*) the segment appendages of the four abdominal segments (Taf. XVI, Fig. 12 *p. n.*). They appear first in the form of cup-shaped sacks which open though a broad mouth. After a further development of the lung-sacks, accompanying which there is an atrophy of the abdominal segments (with the exception of the second pair [of appendages] of the same), they become more roomy and deeper. But first in the latest embryonal stages (Taf. XVI, Fig. 14, from the ventral, Fig. 15, from the dorsal surface) there grows up out of the dorsal part of the lungs a blind tubular passage, whereby also within the lung sacks begins the formation of the leaves. The external gill-opening becomes by this time considerably smaller. The walls of the embryonal lungs consist of a cylindrical epithelium on whose inner side becomes separated a fine cuticula. Moreover, here and there on the outer surface of the lungs are certain groups of cells which evidently belong to the mesoderm.

Although Metschnikoff carefully describes and figures the mode of origin and process of invagination of the book-lungs he does not entertain the idea that they are modifications of the transitory abdominal appendages under which they arise.

* From a taxonomic point of view too much dependence must not be placed on the position and arrangement of the gills or respiratory organs in any class. For example, in Scutigera, a Myriopod, the tracheæ are grouped into structures like book-leaf tracheæ placed in a row down the median dorsal line. These lungs project into the pericardium and thus aërate the blood. (See Sinclair, "A new mode of respiration in the Myriapods," Ann. and Mag. Nat. Hist. March, 1892. See also Voges's Das Respirations-System der Scutigeriden, Zool. Anzeiger, V, 1882, pp. 67–69. Also E. Tömösváry, Ueber das Respirationsorgan der Scutigeriden (Vorläufige Mittheilung) Math. Naturw. Ber. Ungarn I. Bd., p. 175-180, Taf. 4, Fig. 1–4, 1882–'83).

In 1871 E. Van Beneden first suggested the homology between the branchial limbs of Limulus and the lungs of Arachnids. (C. R. Soc. Ent. Belgique, 1871.) He afterwards (1882) reaffirmed this view. In his second paper he derives the Arachnida from the Pœcilopodes (Limulus).

Salensky, according to the abstract in Jahresb. üb. Anat. u. Phys., as early as 1871, stated his belief that, in the spider whose embryology he studied, the third and fourth pairs of provisional abdominal appendages became spinnerets, while the two anterior pairs developed into lungs.

The following is a translation of what is said by the reporter:

The first pair of abdominal legs are transformed into lungs; the special details of this process of transformation are not wholly understood by the author. The second pair of abdominal legs become flatter, broader, and modified into a vascular sinus, in which the cells of the inner germ-layer are changed to blood-corpuscles. The third and fourth pairs of abdominal legs form the germs of the spinnerets; between the third pair arise two new hook-like projections becoming a third pair of spinnerets (p. 324).

In his valuable Recherches sur l'Anatomie des Limules (1872) A. Milne-Edward thus refers to the homology between the gills of Limulus and the lungs of the scorpion:

Les membres abdominaux des Limules sont, comme on le sait, élargis en forme de lames, et ceux de la première paire, tout en servant d'opercule pour clore en dessous la fosse respiratoire, portent les orifices génitaux, tandis que les membres des quartre paires suivantes donnent naissance à autant de branches multifoliées. Chez les scorpions, il n'y a rien qui rappelle les appendices operculiformes dont je viens de parler, et les orifices génitaux sont situés un peu plus en avant à la partie sternale de la région thoracique; mais il y a une grande ressemblance entre les cinq paires de fausses pattes branchiales des Limules et les quatre paires de poches pulmonaires des scorpions; il y aurait même presque identité si, chez des Limules, ces appendices, au lieu d'être libres par leurs bords latéraux aussi bien qu'en dessous, contractaient avec les parties voisines du test des adhérences, de façon à ne laisser d'ouverture que sous leur bord inférieur, et si les feuillets branchiaux de ces animaux, au lieu d'être imperforés, se creusaient d'une cavité accessible à l'air, à peuprès de la même manière que les fausses pattes branchiales des Tylos et des Porcellions se creusent de poches pulmonaires. Si la forme organique réalisée par les Limulus, au lieu d'être appropriée à la vie aquatique, s'adaptait à la respiration aérienne d'une manière analogue à ce que nous savons exister chez certains représentants terrestres du type dont dérivent les Crustacés isopodes à respiration aquatique, il n'y aurait donc, sous ce rapport, aucune différence importante entre ces deux sortes d'animaux articulés (p. 56).

Balfour, in his "Notes on the development of the Araneina" (1880), does not refer to the book-lungs or to their mode of origin. In speaking of the four pairs of rudimentary abdominal appendages, he remarks:

The four rudimentary appendages* have disappeared, unless, which to me seems in the highest degree improbable, they remain as the spinning mammillæ, two pairs of which are now present.

Balfour's observations were made on *Agelena labyrinthica*.

In his essay entitled "Limulus an Arachnid," Lankester, in 1881, following A. Milne-Edwards, adopts the homology of the book-lungs of the Arachnida with the branchial legs of Limulus. He was apparently ignorant of, or had overlooked, Salensky's opinion that the last two pairs of embryonic abdominal appendages of the spiders become the spinnerets. Lankester remarks:

When we examine the sternal area of the segments of Limulus which carry lamelligerous appendages, we find that, although the integument is mostly soft and flexible, yet there are small sclerites present, *and in fact stigmata or apertures leading into pits corresponding to the stigmata of the pulmonary sacs of Scorpio.*

These "muscular stigmata" are then described in detail, followed by a hypothesis of the mode of origin of the book-lungs from branchiferous limbs like those of Limulus, which was afterwards abandoned by the author. We opposed this hypothesis in a critique of Lankester's paper (Amer. Naturalist, April, 1882) and suggested a difficulty in the acceptance of this view when the gill-plates of the Eurypterida are taken into account, these being arranged somewhat like the teeth of a rake. Lankester also expresses the opinion that the Arachnida through the scorpions were derived from the Merostomata, and that it is not possible to place the scorpions and the Merostomata in separate classes (p. 82).

MacLeod (1882) regarded the lungs of the scorpion as the homologues of the gills of Limulus, but explained the mode of transformation of gills into book-lungs differently from Lankester.

He regards the two structures as homologous and explains the transformation of the Limulus gills into lungs in the following way: The lengthening of the abdomen of Limulus had the result that the abdominal gill-bearing limbs were no longer covered; hence a part of each gill-bearing limb coalesced with the integument of the abdomen and then respiratory cavities came to exist. When this kind of Limulus became adapted to a terrestrial life, the gill-leaves, no longer supported

*He undoubtedly meant to say four *pairs* of rudimentary appendages, as he figures them (Figs. 5 to 8*a*, 8*b*).

by the water, must have simultaneously become soldered by their edges to the walls of the gill-chamber.

For our earliest information regarding the mode of development of the lungs of spiders we are indebted to Schimkewitsch (1885). He states:

Balfour has shown* that the tracheæ and lungs of Araneina are formed by the invagination of the ectoderm. I am unable to confirm this observation. In the embryo of *Lycosa saccata*, before hatching, the tracheæ are represented by a principal trunk from which arise four secondary branches. Their wall is formed of the epithelial ectodermic layer lined by a homogeneous internal coat and covered by an external coat containing nuclei of mesodermal origin (V, chap. III). In this same stage the structure of the lungs is very interesting (Pl. XXII, Fig. 1, *pm*). A. Milne-Edwards and J. MacLeod have endeavored to prove the homology of the lungs of Arachnida with the gills of Limuli. The lungs of the embryo of *Lycosa saccata* consist of true tracheæ arranged in bundles; the principal trunk (Pl. XXII, Fig. 1), which opens outward by the stigmatic orifice (*st*), divides into five secondary branches. The epithelial layer of these last is represented by flattened cells. The secondary branches, flattened from above downward, enter the cavity surrounding the lungs, and in the spaces between these are to be seen the blood corpuscles. Thus the embryonic lung consists of a trachea arranged *en faisceau;* the only difference to be noted is the absence of the external tunic, which I have not observed, either on the lung of the embryo or on that of the adult (p. 561).

In the following year, in his "Les Arachnides et leurs Affinités" (1886), he reiterates this view.

In the same year, Locy, in his "Observations on the development of *Agelena nævia*," gives a still more complete account of the mode of origin of the lungs of spiders, with excellent figures. He states that the lungs arise as a pair of extensive invaginations at about the same time as the proctodæum. "In sagittal sections of early stages the lungs appear as oblong plates of cells, the large oval nuclei of which are arranged in parallel rows." The flattened sacs are hollow and divided at intervals by 2-cell columns, the interspaces sometimes containing blood corpuscles. The details are mostly histological and the author does not enter into any morphological comparison with the book-lungs of Limulus, but nothing is said contrary to the view that the lungs are a bundle of tracheæ.

In his paper "On the origin of vertebrates from Arachnids" (1890), Patten refers to the chitin-lined tubes of the scorpion, "which serve for the support of muscles." These, as we understand them, are the "muscular stigmata" of Lankester and occur in insects as well as in Arachnida and Podostomata, as we have observed them in a specimen of Asaphus as well as in Limulus. As Patten remarks: "The chitinized tubes are comparable with the three or four pairs of tracheal invaginations which in insects give rise to the tentorium." He then adds:

I regard the lung-books of scorpio and the chitin-lined tubes described above as belonging to the same category, for after careful study I have found nothing to indicate that they arise as modifications of rudimentary abdominal appendages (p. 355).

In 1885 Lankester discards his first hypothesis, which he regards as "overstrained," and replaces it by a second "perfectly simple" one.

In his notes on the embryology of Limulus (1885) Kingsley describes the early stages of the abdominal limbs and discusses at some length their homology with the "pulmonary books" of Arachnids, and he admits its general validity, though not ready "to follow all of Prof. Lankester's intermediate steps, nor those of MacLeod." His hypothesis and figures are ingenious and more simple than those of Lankester. As he remarks:

As I have mentioned above, the process of formation of the gill-leaves is largely by a process of outgrowth, but there is also a slight ingrowth, especially noticeable at the distal portion of the appendage. This, however, disappears with growth, but is very noticeable in all my sections. To transform the gill of Limulus into the lung of Scorpio it is only necessary that, together with the sinking of the whole organ, as described above, the inpushings of the integument to form the lamellae should be exaggerated and the outgrowth correspondingly decreased. On Pl. XXXVII, Figs. 18 to 20, I have diagrammatically illustrated the steps in the process, the gill-leaves being few in number to secure clearness. In 18 we have the typical condition found in Limulus, one appendage being shown half in section and half in perspective. In 19 we have an intermediate condition, when, as suggested above, the animal was leaving the water and seeking a terrestrial life. Here the gill-bearing appendage (*ga.*) is partially sunk in the surrounding tissues to secure protection. The same causes would also tend to produce a similar change in the gill leaves (*gl.*) and they would also tend to be formed rather as ingrowths than as protruding processes. This change in structure would be the more readily effected on account of a change of the medium of respiration. A gill needs either to project into the water or to have some means of instantly changing the fluid which bathes it. An organ for aërial respiration, on the other hand, is not so restricted in its position, since the air is more fluid and more elastic and hence more readily changed. Another advantage to the animal resulting from the change is that the oxygen is thus brought nearer to the tissues requiring it.

* I can find no reference in Balfour's memoir to this subject.

In Fig. 20 we have a diagrammatic representation of the pulmonary sac of the Arachnids. The appendage (*ga.*) has now become sunk in the body and the hole through which it passed is the stigma (*stg.*). The gill-lamellæ have entirely disappeared and the pulmonary ones (*pl.*) have taken their place. The process here described is different from that imagined by MacLeod. It accords more with the development of the gills in Limulus and avoids the necessity of union of the gill laminæ and the expansion of the sternum.

But the most convincing and direct proof of the conversion of a portion, not all, of the temporary embryonic abdominal limbs of the Arachnids into lungs has been afforded us by the statements and figures of Kishinouye in his essay "On the development of Araneina," 1890. As will be seen by the following extract, the view also suggested to us by Metschnikoff's description and figure is that the *entire appendage is not converted into the book-lung.* Kishinouye also states unqualifiedly that the third and fourth pairs of abdominal appendages are transformed into spinnerets. His drawings (Fig. 34) directly confirm this and establish the truth of Salensky's supposition.

In the basal part of the first abdominal appendage of each side there arises an ectodermic invagination, whose opening faces away from the median line. It is neither deep nor spacious, but is a little pocketlike invagination. This is the beginning of the lung-book.

The development of this organ, briefly stated, is as follows: Of the wall of the invaginated pocket, that which faces the distal end of the appendage is much thicker than the opposite wall, filling the interior of the appendage. The cells composing it become after a while arranged in parallel rows (Figs. 34 and 47). Each two of these parallel rows adhering together produce the lamellæ of the lung-book. The external epithelium of the appendage which cover these lamellæ becomes the operculum of the lung-book after it is depressed in height. Judging from figures (Figs. LXXIX and LXXIX′) given in his essay "On Insects and Arachnids," Bruce seems to have mistaken the caudal prominence of the early period of this stage (see my Figs. 24–28) as the operculum of the lung-book. According to him the abdominal appendage is invaginated to form the lung-book; but as we have seen, it is not so. Locy has correctly described the formation of the lung-book lamellæ. He says that the lungs arise from infoldings; but he is silent about the place where these infoldings arise.

In the basal part of the second abdominal appendage on the interior side, another ectodermic invagination is produced. It assumes the shape of a deeply invaginated tube and remains in this condition till after the time of hatching. The appendage itself is not invaginated and becomes from this time gradually shorter.

It is very probable that the lung-books were derived from the gills of some aquatic arthropodous animal such as Limulus, for the lung-books are nothing more than the lamellar branchiæ of Limulus sunk beneath the body surface. The tubular trachea may afterwards have been derived from the lung-books. The branchial lamellæ of Limulus are formed as outgrowths of the ectoderm at the lower (posterior) surface of abdominal appendages, and those of spiders are also produced really in the lower surface of the first abdominal appendage (in the dipneumonous spider). Hence, I think that the spider with two pairs of lung-books is the most primitive one, and the one with one pair of lung books and the other pair transformed into the tubular tracheæ is more primitive than the spider with only one pair of lung-books. I cannot agree with the view of some authors who maintain that the lung-book is derived from a cluster of tracheæ.

The third and fourth pairs of the abdominal appendages are modified into spinning mammillæ (Pl. XV, Fig. 34). At the distal end of each of these appendages a solid proliferation (*sp. gl.*) of ectodermic cells is formed. This becomes the spinning gland. Spiders have generally three pairs of spinning mammillæ, two of which are modified abdominal appendages, while the remaining one is added very late, after the hatching of the embryo. The primitive spider must have had only two pairs of spinning mammillæ. Some tetrapneumonous spiders have only two pairs.

Laurie (1892) accepts MacLeod's thory "in its main lines," but suggests that "the lung-books of the Arachnids were probably derived from a series of paired plate-like appendages, not united in the middle line by a gradual fusion of their edges with the abdominal walls of the body."

Bernard (1892) thinks the fascinating and seductive theory of MacLeod and others will have to be "given up in view of the great morphological difficulties which they involved" (Spengel's Zool. Jahrbuch, 1892), the main reason he gives being that in Galeodes it is difficult to believe that the thoracic and abdominal stigmata had a separate origin.

If now we return to Metschnikoff's description and figure of the mode of origin of the book-lung of the scorpion, it will be seen that, as he states, the stigmata arise directly under the temporary leg, as seen in his Fig. 12, Taf. XVI. The invaginated portion, then, does not represent the entire leg, but a part of it, possibly the epipodal, which represents the branchial or outer division of the gill-bearing leg of Limulus. The inner portion of the scorpion's leg then disappears by absorption.

THE DEVELOPMENT OF THE BRANCHIAL LEGS OF LIMULUS.

Our own observations on the branchial legs are fragmentary and have been made on embryos of a stage nearly that represented by Fig. 20, Pl. IV, of our first memoir, this stage being marked by the appearance of the third pair of abdominal limbs.

At this stage the appendages are very thick and like loose flattened sacs, and the abdomen beyond is loose and baggy.

My sections were sagittal ones, and, though made on freshly preserved material, were not so satisfactory or desirable regarding histological details as could be desired.

The "operculum" or first pair of abdominal legs are thicker, though but little longer, than the second pair. Seen in section on the slide, the limb is simply sack-like, with no internal structures or any hairs externally, though the musculature is in part developed. The second pair alone bears the gills; the appendage itself is nearly, if not quite, as long as the first pair, though not so thick. The muscles are distinctly developed. The legs each bear five leaf-like sacs (Figs. 2, 3, 4, 5, *a*, *b*, *c*, *d*, *e*), which are from one-half to two-thirds as thick as the leg itself, and gradually diminish in length, the outside one, which is the last to be developed, being minute, the two basal ones being of nearly equal length and from a third to a fourth as long as the entire limb. The gills are hollow, but lined with hypodermic cells, though the nuclei are not visible, this being perhaps due to the mode of preparation or of sectioning. The limits of the cells themselves are not visible, and from the thick protoplasmic, very transparent lining, which does not readily stain with the alcoholic carmine, more or less conical, pointed processes extend out into the cavity, and sometimes meet similar processes from the opposite side, forming slender pillars or trabeculæ. These thin protoplasmic partitions, though suggesting the regular transverse septa of the spider's lung-lamellæ, described and figured by MacLeod * and by Locy, are by no means so distinctly developed and are not morphological equivalents to them. The short outer leaves are more or less crumpled, with very thin walls.

The larvæ (Pl. XX, Figs. 6, 6*a*, 6*b*, 6*c*) were prepared, sectioned, and mounted in the same manner as the embryos, but the histological structure of the gill-sacs is now much more definite and satisfactory to study, the hypodermis consisting of distinctly marked cells, with large deeply stained nuclei.

The first pair of abdominal legs reach to the end of the abdomen, as already described and figured in my first memoir, and also more elaborately by Dr. Kingsley. They are seen in section to be very thin, being in this respect much as in the adult.

The second pair of legs (Fig. 6*b*, 6*c*, I) is only about half as long as the first pair. The hypodermis towards and at the base consists of large distinct columnar cells, becoming at the base double. Under the hypodermis, at the base of the appendage, is a double series of rounded, quite large cells; while within the interior is filled with nuclei of irregular size, arranged in short streaks, the cell-walls being obliterated. Pl. XX, Figs. 6*a*, 6*c*, show five leaves or gill-sacs lined with a hypodermis as distinct as in the appendage itself. The basal or first-formed gill-sac is nearly twice as long as the second one; the succeeding ones diminish in length, the fifth one being a simple fold.

There are no traces of any transverse septa comparable with those of the lung-leaves of Arachnida.

The third pair of appendages (Pl. XX, Fig. 6*c* III) is now simple, not standing out free from the surface, but lying under the second pair. The cells of the hypodermis are large and round, not closely packed and columnar, as in the second pair. As yet there are no rudiments of the gill-sacs. The cells which are to give rise to them are as yet in an indifferent state, and this condition of things, shown in our figure, strongly recalls the structure of the embryonic appendages destined to form the book-lungs of the spider represented by Kishinouye. (His Fig. 34, 1 abd. app., 2 abd. app., etc.)

This striking similarity in the shape of the deeply stained nuclei and their arrangement just as the book-leaves or sacs are beginning to be formed shows the close similarity of the mode of origin of the appendages in question of the two groups.

Further observations, both on the embryonic as well as larval structure of Limulus and of Arachnids, are now needed to finally clear up the points which have been raised by recent investigations. But Kishinouye's statements and his Fig. 34 have, more than any others, convinced

* MacLeod has studied the gills of the adult Limulus by sections, and finds that the inner cavity of a gill-sac is lined entirely with hypodermic cells and has fibrous pillars, besides numerous multicellular glands opening on its upper surface. On the other hand, a single leaf of a spider's lung has within it numerous transverse pillars (querpfeiler), each with two nuclei, and a peculiar modification of the plasma, which perhaps acts as a muscle to contract the cavity of the leaf. Other cell elements are wanting. (Arch. Biol. v., 1–34, 1884).

me that the book-leaves of Arachnida are really the homologues of the thin gill-sacs of Limulus, and that the two classes have probably originated, if not from a common ancestor, yet from those standing very near each other.

In closing, we would make a suggestion in the way of an explanation of the points of resemblance of the Podostomata (Merostomata and Trilobites) to the Phyllopod Crustacea, especially Apus. Even so strong an opponent of the idea that there is any close affinity between Apus and Limulus as Lankester, allows that there are some points of resemblance between Apus and Limulus, "the most important being the jaw-processes at the base of all the ambulatory limbs, and the presence of a pure archicerebrum in both genera."

We have shown that the brain of Limulus, though roughly speaking an archicerebrum, is very different from that of any Phyllopod. Still the points of resemblance between these primitive Phyllopods and the Merostomata are due, perhaps, to the fact that the ancestors of both Crustacea and Podostomata were probably derived from somewhat similar Annelid-like ancestors, though by quite independent lines of descent. We would therefore agree with Lankester's conclusion in his essay on Apus, that the points in which Apus and Limulus agree "are probably points in which they both approach the common ancestor of the Arachnida and Crustacea."

But we differ from this able author in supposing that the Merostomata and Trilobites, or at all events the Merostomata, should be merged with the Arachnida, as they have characters, both external and internal, which forbid their being regarded as Arachnids.

We believe, with A. Milne Edwards, that they should form a separate class. There were, then, four lines of development in the Arthropoda (throwing out for the present the Linguatulina and Tardigrada), viz: The Podostomatous line, the first to be struck off from the Annelidan stock (the trilobites being the first forms to appear), second the Arachnidan line; third, the Crustacean line, nearly coeval with the first or Podostomatous; and the fourth, the line culminating in Myriopods, Scolopendrella, and insects; and it is safe to suppose that the terrestrial tracheate groups of Arachnida, Myriopoda, and insects were later products than the marine, aquatic branchiate classes, *i. e.*, the Podostomata and the Crustacea.

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LETTERING OF THE PLATES.

Ab I, Ab II, Ab III, first, second, and third pairs of abdominal appendages of the embryo. Pl. XVII.
an., anus (=proctodæum). Pl. XVII.
ant. st., anterior branch of the stalk of the mushroom body.
1st app. gang., ganglion of the first pair of appendages.
app.' n., nerve of 1st pair of appendages ("cheliceral nerve").
asc. st. m. b., ascending branch of the stalk of the mushroom body.
b. c. l., bulb of the cerebral lobe ("*tubercle protocerebrale*" of Viallanes.
br., brain.
c. g. c., *c. g. c'.*, *c. g. c''.*, groups of cerebral-ganglion cells.
ch. c., chromatic cells, small ganglion cells, or aprotoplasmic cells of the mushroom body.
c. l., *cer. l.*, *cer. lobe*, and *cer. gang.*, cerebral lobe or ganglion.
e. ch., "Chiasma," or bundle of twisted nerve-fibers connecting the outer or third with the second division of the lateral-eye lobes ("*Chiasma externe*" of Viallanes).
c. com., *c. l. com.*, and *com. c. l.*, cerebral commissure.
f., sense organ of embryo. Pl. XVII.
f'. f''., bundles of fibers arising from large ganglion cells. Pl. VI.
fasc., fascia or bundle of fibers arising from the ganglion cells.
g. 1st app., ganglion of the first pair of appendages.
i. g. l., inner ganglionic layer of lateral eye lobes.
l., labrum of embryo. Pl. XVII.
lat. h., "lateral heap," or "dorsal organ" of the embryo. Pl. XVII.
lat. eye l., lateral-eye lobe.
lat. eye l^1., proximal or first division of the lateral-eye lobes.
lat. eye l^2., second or middle division of the lateral-eye lobes.
lat. eye l^3., third or external division of the lateral-eye lobes.
lat. eye n., lateral-eye nerves.
lat. eye n. r., origin or root of lateral-eye nerve.
l. g. c., large ganglion cells.
l. st., lateral branch of stalk of mushroom body.
l. t. n., *l. teg. n.*, lower tegumental nerve of the brain.
m., mouth of the embryo (stomodæum).
m. b., mushroom body or pedunculated body.
m. eye l., median-eye lobe.
m. eye n., median-eye nerve.
m. eye n. e., external lobule of the median eye-lobes.
m. eye n. r., root of median-eye nerve.
m. n., unpaired fronto-median nerve situated between the lower tegumental nerves.
œ., œsophagus.
n^1. to *n*^{9}. neuromeres, or ganglia of the embryo.
œ. com., œsophageal commissure or connective.
post. œ. com., postœsophageal commissure. Plate XVI.
pr. œ. com., preœsophageal commissure. Plate XVI.
st., stomach. Pls. XVIII and XIX.
st. mb., stalk of the mushroom body.
s. m. g. c., *s. m. g. c'.*, small ganglion cells forming the ruffle-like masses of the mushroom body.
teg. n., tegumental nerves of the œsophageal ring.
u. teg. n., upper tegumentary nerve.
I, II, III, IV, V, VI, the six pairs of cephalothoracic appendages.
I g., *VI g.*, ganglia of the first and sixth pair of appendages.

EXPLANATION OF PLATES.

PL. I. Figs. 1–7. Horizontal sections through the brain of the adult Limulus passing from above downwards, involving the lateral eye and median-eye lobes. In Fig. 5 the section involves the upper part of the median-eye lobes (*m. eye l.*); the ruffle-like masses of the mushroom bodies (*m. b.*) are seen in Fig. 1, on the right side, this and all the sections of this brain having been cut a little obliquely, the brain not having been evenly placed in the object-holder.

PL. II. Figs. 7*a*, 7*b*, 8–10. Horizontal sections, continued, passing downwards through the same lobes. Fig. 7*a*, represents the same section as Fig. 1, but enlarged; *ch. cl.*, the internal thin sheet of chromatic or small ganglion-cells situated at the distal end of the external chiasma of the lateral-eye lobe. (Compare Pl. VII, Fig. 2*a*, *ch. cl.*). Fig. 7*b*, the external or third division of the same lobe ("*lame ganglionnaire*" of Viallanes), still more enlarged showing the inner sheet of chromatic cells (*ch. cl.*) and the fibrillæ arising from them. Fig. 8, from a section lower down, passing through the median-eye lobes (*m. eye l.*) and involving on the right side the first and middle divisions of the lateral-eye lobe; *m. b.*, the upper masses of chromatic cells of the mushroom body; *app'. n.* nerve of the first pair of appendages; *m. eye n.*, median-eye nerves fused into one. Fig. 9, the same a little lower down. Fig. 10, details of the median-eye lobes; *m. eye n. r.*, root or origin of the median-eye nerves, seen to be separate from its fellow, and to arise from near the external aspect of the lobes, while still more externally arise the lateral projection of the lobes (*m. eye n. e.*) the fibers arising from a special mass of chromatic cells. (See also Pl. VII, Fig. 1, *m. eye n. r.*) The space between the roots of the median-eye nerves is seen to be filled with both large and small (chromatic) ganglion-cells; *c. com.*, the cerebral commissure, the fibers of which appear to arise from the crescent-shaped mass of chromatic cells.

PL. III. Figs. 11–15. Horizontal sections, continued, passing through the median-eye lobes. Fig. 11. This section passes through the cerebral commissure (*c. l. com.*) with its crescent-shaped mass of chromatic ganglion cells. Fig. 12. The œsophageal commissure connecting the cerebral commissure with the œsophageal ring is seen on the right side of the section.

PL. IV. Figs. 16–19. Passing through the cerebral lobes. In Fig. 17 is seen a portion of the stalk of the mushroom body (*st. m. b.*). Fig. 18. Enlarged view of a bundle of fibers on right side of the cerebral lobes, arising from a group of chromatic cells. Fig. 19. Enlarged view of a similar area in a section below.

PL. V. Figs. 20–22. Sections passing through the lower part of the cerebral lobes and their "nucleogenous bodies," forming the cortical portion of the numerous branches of the mushroom bodies. In Fig. 21 is seen the basal portion of the stalk of the left mushroom body, with one of its lateral branches (*l. st.*) and the anterior branch (*ant. st.*). (Plate XXXI is photographed from a drawing of a section lower down, below the cerebral lobes; the clear spaces being the fibrous substance of the branches of the mushroom body which pass down to the base of the brain, and which, with their ganglionic cortices, form the lower third of the brain.)

PL. VI. Fig. 1. Horizontal section (Nos. 43 and 44) through the brain of a small Limulus, the body about 2 inches long, exclusive of the caudal spine, and showing the entire lateral eye lobes; *f'.*, a bundle of fibers arising from the large ganglion cells in the median-eye lobes and passing backwards into the cerebral lobes, meeting the fibers of its mate; *f''.*, a second bundle of fibers meeting those of its opposite bundle in the middle of the cerebral lobes; *ch. c.*, sheet of chromatic cells in the external or third division of the lateral-eye lobes. At this stage the ganglia of the first pair of appendages are seen to be entirely distinct from the brain proper, not showing the tendency to fuse with the base of the brain, seen in old, large examples.

PL. VII. Figs. 1–3. The same lower down. Fig. 1. Origin of the median-eye nerves; the horseshoe-shaped bundle of fibers inclosing the large and small ganglion cells of the partially fused median-eye ganglia or lobes. Fig. 2. The entire lateral-eye lobe is seen on the right side; *l. g. c'''.*, a group of large ganglion cells sending a bundle of fibers backward into the œsophageal commissure. Fig. 2*a*, showing at *e. ch.* the twist or "chiasma" (*sic*) of the fibers connecting the second and third divisions of the lateral eye ganglia, and the sheet of chromatic cells which appear to give rise to the fibers forming the so-called chiasma.

PL. VIII. Figs. 1–4. Horizontal sections of the same. Fig. 1. Section passing through the base of the cerebral ganglia and involving the lower tegumental nerves, or nerves to the sensorial papilla situated in front of the first pair of appendages (probably the "neuropore" of Patten). Figs. 2, 3, and 4, sections passing through the lower branches of the mushroom bodies. Figs. 5, 6, 7, sagittal sections of brain of a small Limulus of the same size as above indicated. Fig. 5, represents a section through the brain passing through the lateral-eye lobe and nerve; also involving the ganglia of the first and of the second pair of appendages, forming the anterior portion of the œsophageal ring. Fig. 6. Section passing through the median-eye lobe and nerve; also the cerebral lobe and the nerve to the first pair of appendages.

PL. IX. Figs. 1–7. Sagittal sections through the brain of an adult Limulus, beginning near one side. In this and plates X to XVI the pink portions represent the cortical masses of small ganglion cells of the mushroom body.

PL. X. Figs. 8–13. The same series continued to the middle of the brain, representing, as before, a selection of the typical sections.

PL. XI. Figs. 1–5, and 7. Transverse (frontal) sections of the brain of an adult Limulus from before backwards.

PL. XII. Figs. 6, 6*a*, 8, 9. The same series continued backwards. Fig. 6*a*. Enlarged view of the left median-eye lobe. Fig. 8. Enlarged view of the median-eye lobes a little further back. The fibers arising from the large ganglion cells pass inward towards the median line of the brain.

PL. XIII. Figs. 10–15. The same series continued backwards.

PL. XIV. Figs. 16, 17. The same series continued. Fig. 18. Transverse section through the brain of a young Limulus, passing through the cerebral lobe, and its commissure; externally is the bulb of the cerebral lobe (*b. c. l.*). From this portion of the cerebral lobes arise the stalk of the mushroom body on each side, sending off descending, lateral and ascending (*asc. st. m. b.*) branches.

PL. XV. Figs. 19, 20. Transverse sections of the same lower down, and involving the œsophagus.

PL. XVI. Figs. 1–12. Transverse sections through brain of a young Limulus, and passing back through the œsophageal ring to the basal portion of the ventral cord. Fig. 6 (section 196), *pr. œ. com.*, pre-œsophageal commissure, connecting the ganglia of the first pair of appendages. It will be seen that in Limuli about two inches in length exclusive of the caudal spine this commissure is quite free from the posterior part of the brain. Compare also Pl. XXXIII. This is apparently the "Commissure deutocerebrale" of Viallanes. See Fig. XIX, p. 312, copied from his work. Figs. 8 to 12 should be turned around, as these sections pass behind the œsophagus. Fig. 8, *post. œ. com.*, represents the second commissure, *i. e.*, the first one behind the œsophagus. Figs. 9 to 12 pass through the beginning of the ventral cord.

PL. XVII. Figs. 1–6. All representing the embryo of a single stage showing the ganglia of the median eyes of the lateral eyes, and the central ganglia. *l.*, labrum. The pit directly in front of the labrum may possibly be the "neuropore" of Patten; n^1 to n^9, the neuromeres, or embryonic ganglia; *f.*, the two pairs of sense or glandular organs visible at this stage; *lat. h.*, the "lateral heap" or dorsal organ.

PL. XVIII. Figs. 1–5. Sections through the larva of Limulus, showing the brain and nerve ganglia. Figs. 6–9. The same of the trilobite stage.

(Compare also the figure of a better section of the larva as a whole in my memoirs published in 1880 in Anniv. Memoirs of Boston Society of Natural History, Pl. III, Fig. 2.)

PL. XIX. Figs. 1–9. Sections through the larva of Limulus.

PL. XX. Figs. 1–6. Sections of the lower part of the body, showing the nervous system and abdominal legs of the trilobite stage. Figs. 6 and 6*a*, 6*b*, 6*c*, sections of the abdominal legs and gill-plates of the early larvæ. Fig. 6, section of the first abdominal leg (operculum), and of the second, bearing five gill-leaves, and the rudiment of a sixth. Fig. 6*a*. The same enlarged. Fig. 6*b* and 6*c*, other sections of the same from the same larva.

All the figures on Plates I to XX have been drawn with the camera by the author.

PL. XXI. From a microphotograph of the section of the brain represented by Pl. I, Fig. 3.

PL. XXII. From a microphotograph of the section of the brain a little below.

PL. XXIII. From a microphotograph of the section of the brain represented by Pl. I, Fig. 6, where the parts are lettered.

PL. XXIV. From a microphotograph of the next section below.

PL. XXV. From a microphotograph of the section represented by Pl. II. Fig 8.

PL. XXVI. From a microphotograph of the section represented by Pl. II, Fig. 10.

PL. XXVII. From a microphotograph of a section still lower down.

PL. XXVIII. From a microphotograph of the second section below Pl. XXVII.

PL. XXIX. From a microphotograph of the section represented by Pl. III, Fig. 12.

PL. XXX. From a microphotograph of the third section below that represented by Pl. III, Fig. 14.

Pl. XXXI. From a photograph of a drawing, by the author, of a section much lower down than that represented by Pl. V, Fig. 22.

PL. XXXII. From a microphotograph of a transverse horizontal section through the brain of a young Limulus, passing through the lower part of the cerebral lobes, with the commissure uniting them and the œsophagus behind. Osmic acid preparation. (Section 136.) (The same section is represented on Pl. XIV, Fig, 18.

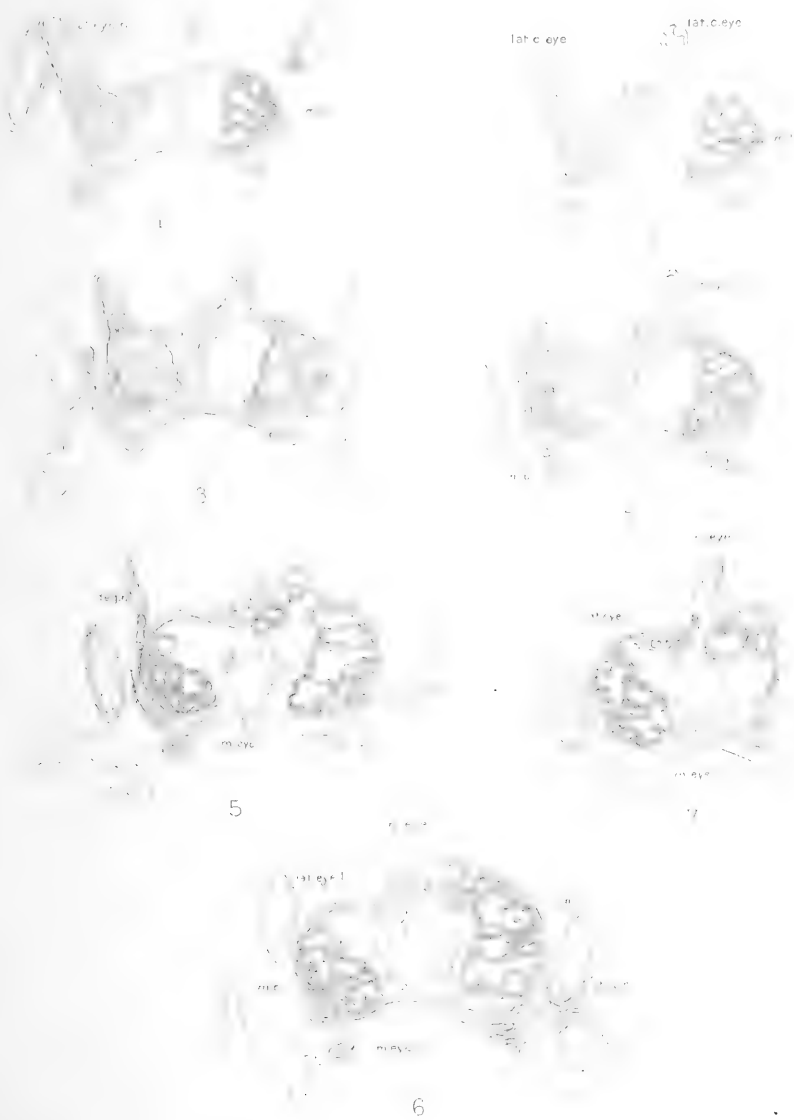
PL. XXXIII. From a microphotograph of a horizontal section through the brain of a young Limulus, involving part of the œsophageal ring and ganglia of the four anterior appendages. (Section 32.)

PL. XXXIV. The same, involving the six ganglia on one side of the œsophageal ring and the origin of the connectives of the abdominal portion of the nervous cord. (Section 40.)

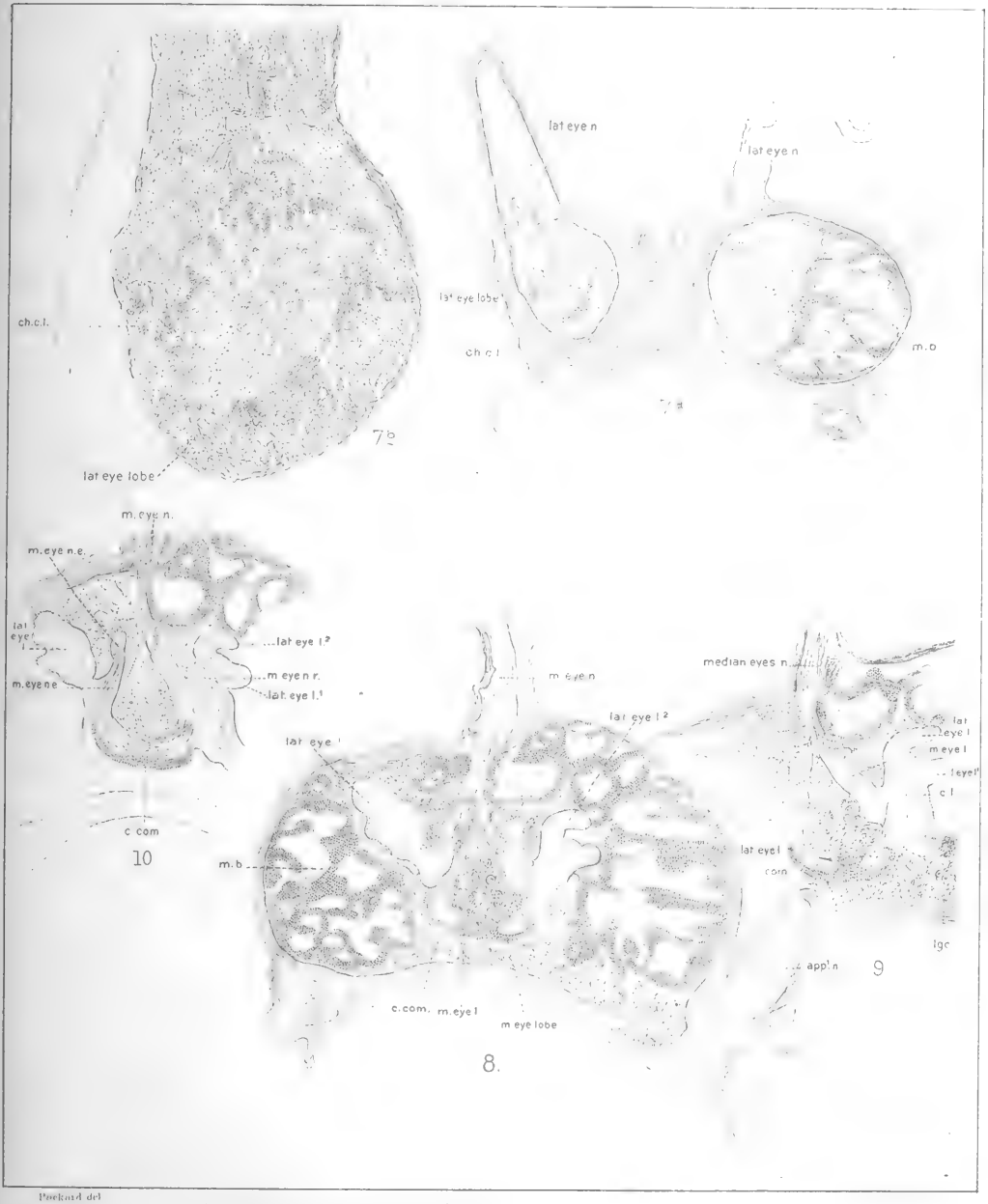
PL. XXXV. The same (section 48) made lower down, showing the same ganglia, with their large ganglion cells, and origin of the nerves to the six cephalothoracic appendages.

PL. XXXVI. Sagittal section through the brain of a young Limulus, showing the dark masses of chromatic ganglion cells contrasting with the fibrous and punctured substance; *con.*, connective passing to the œsophageal ring. (Section 39.) All the microphotographs were taken by Dr. W. M. Gray, U. S. A.

END OF VOL. VI.



Horizontal sections of the brain of Limulus polyphemus



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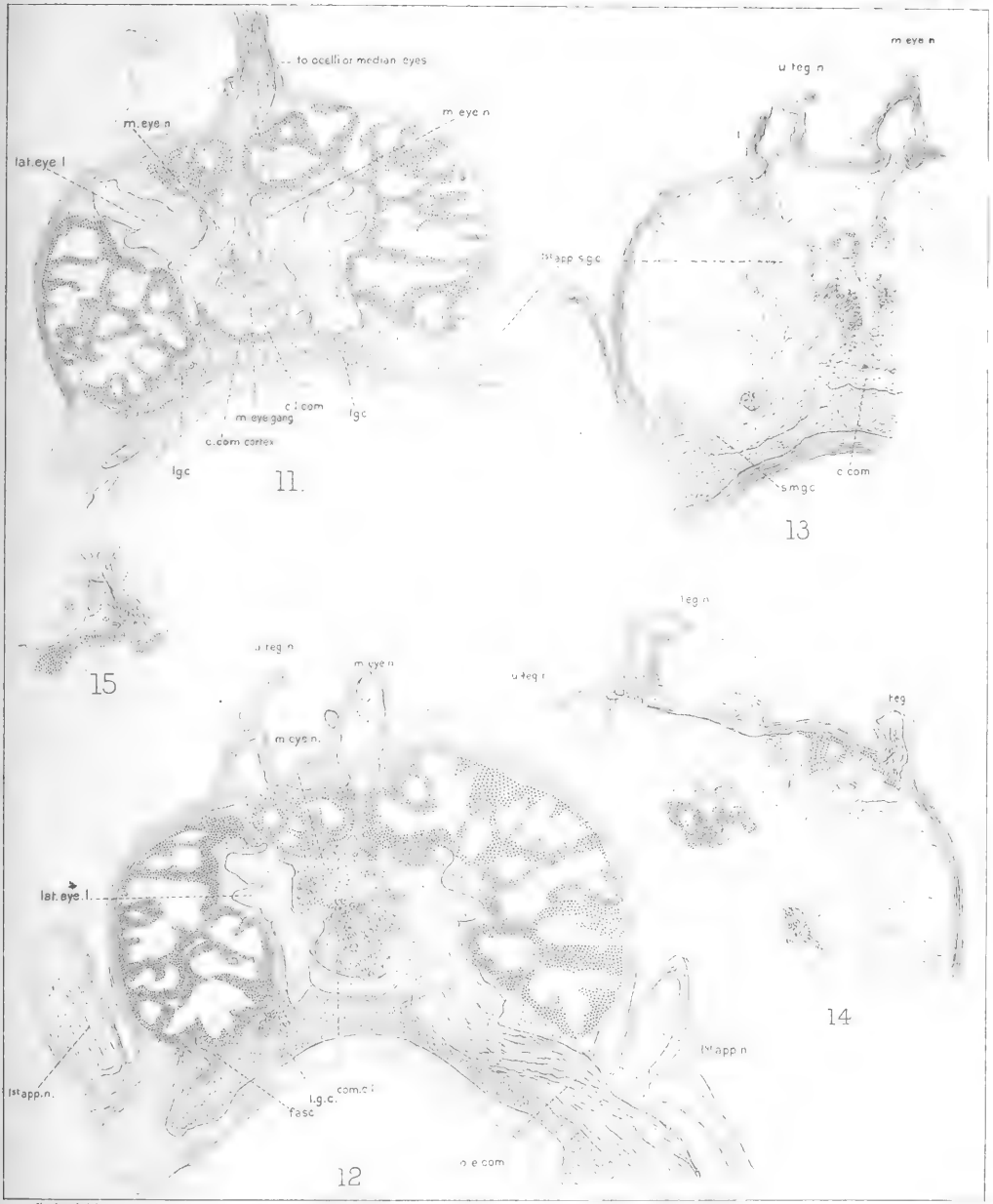
Horizontal sections of the brain of Limulus polyphemus.



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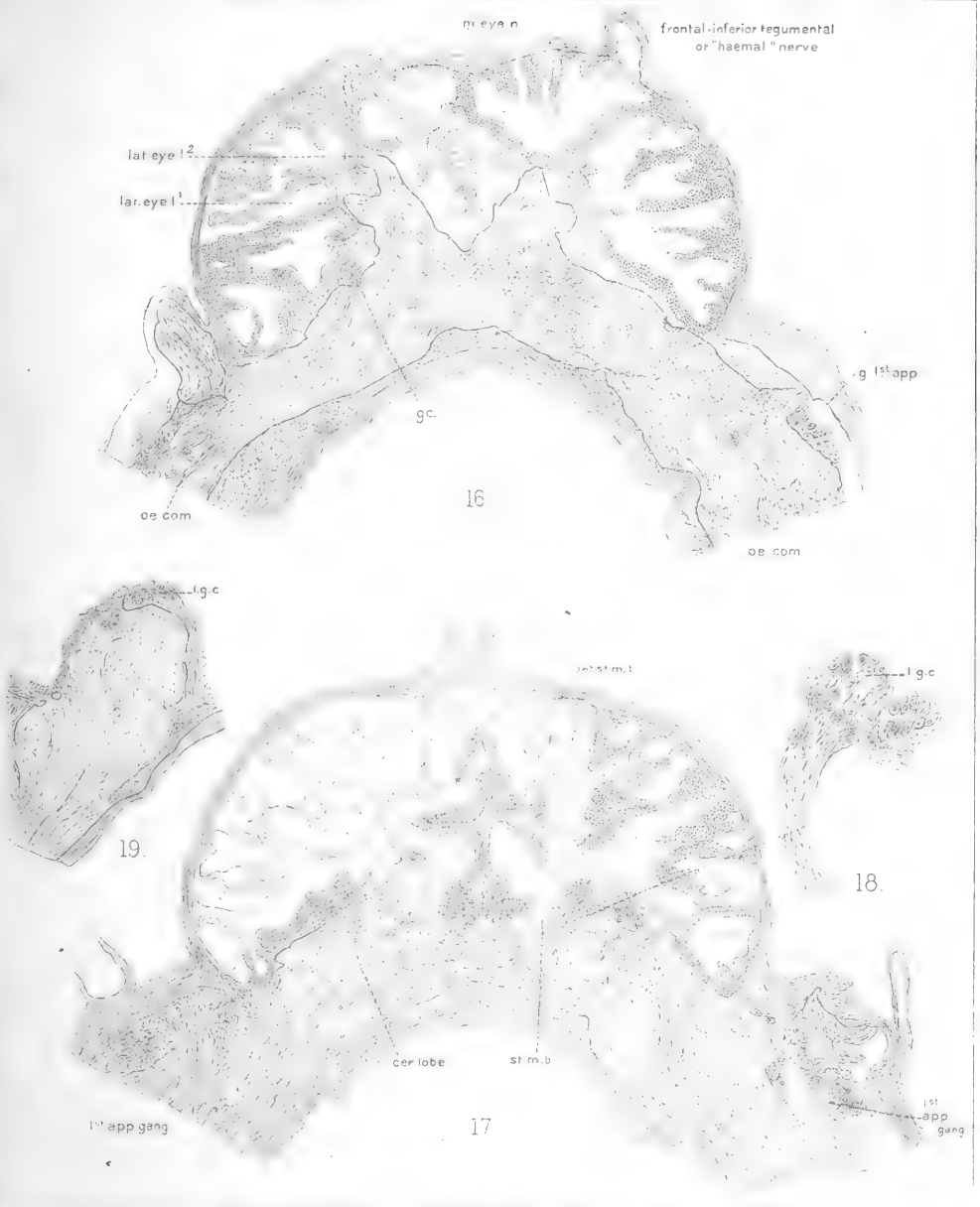
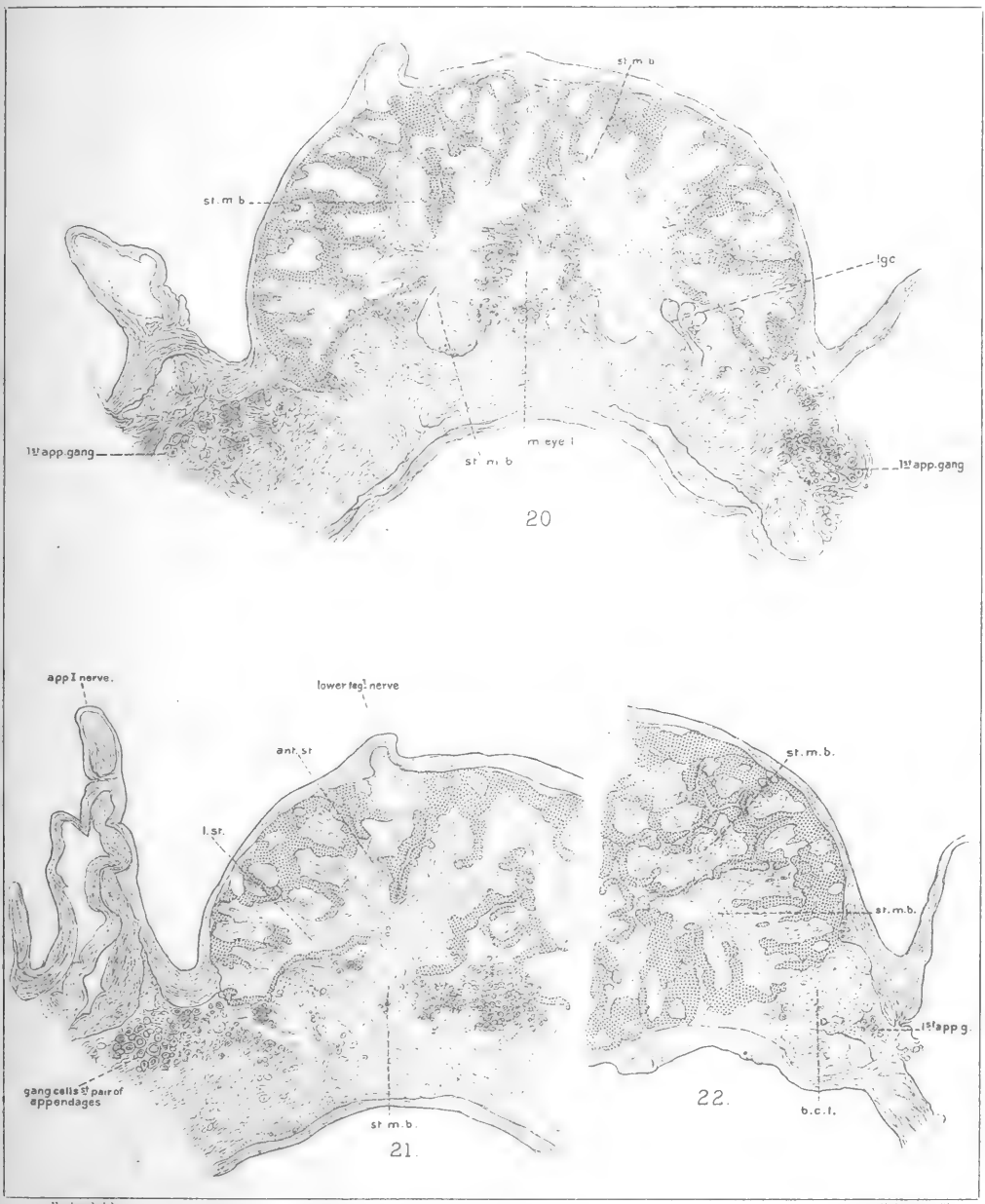
Horizontal Sections of the brain of Limulus polyphemus.



Horizontal Sections through the brain of Limulus.



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Horizontal sections through the brain, of Limulus.

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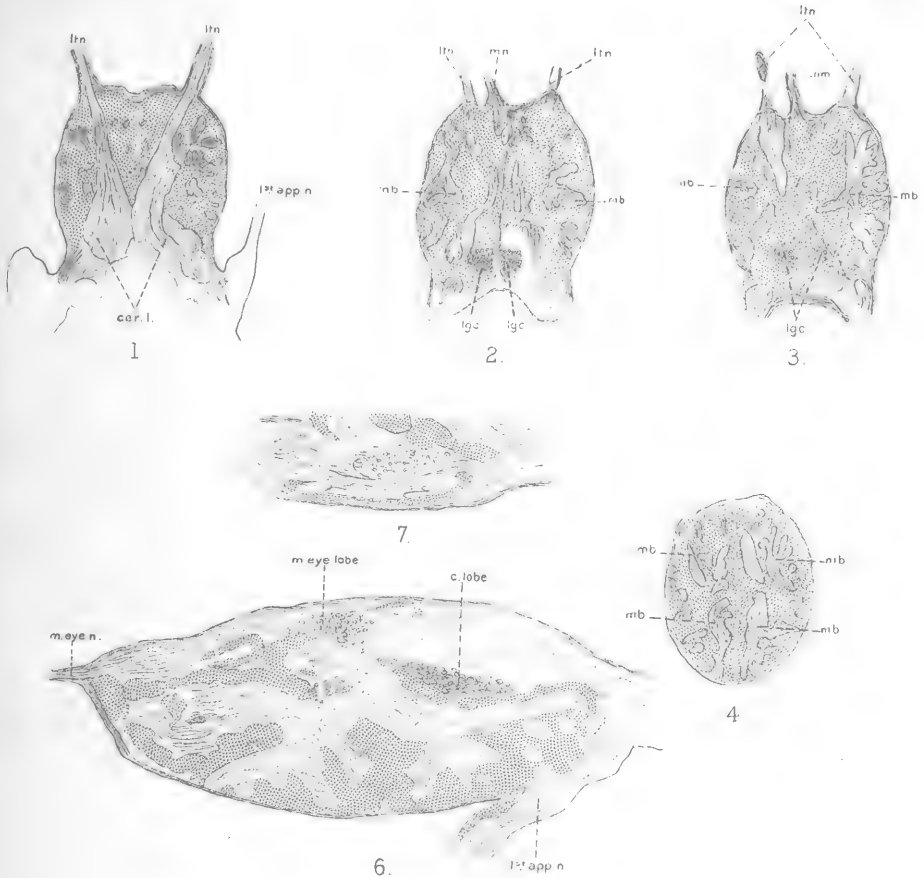
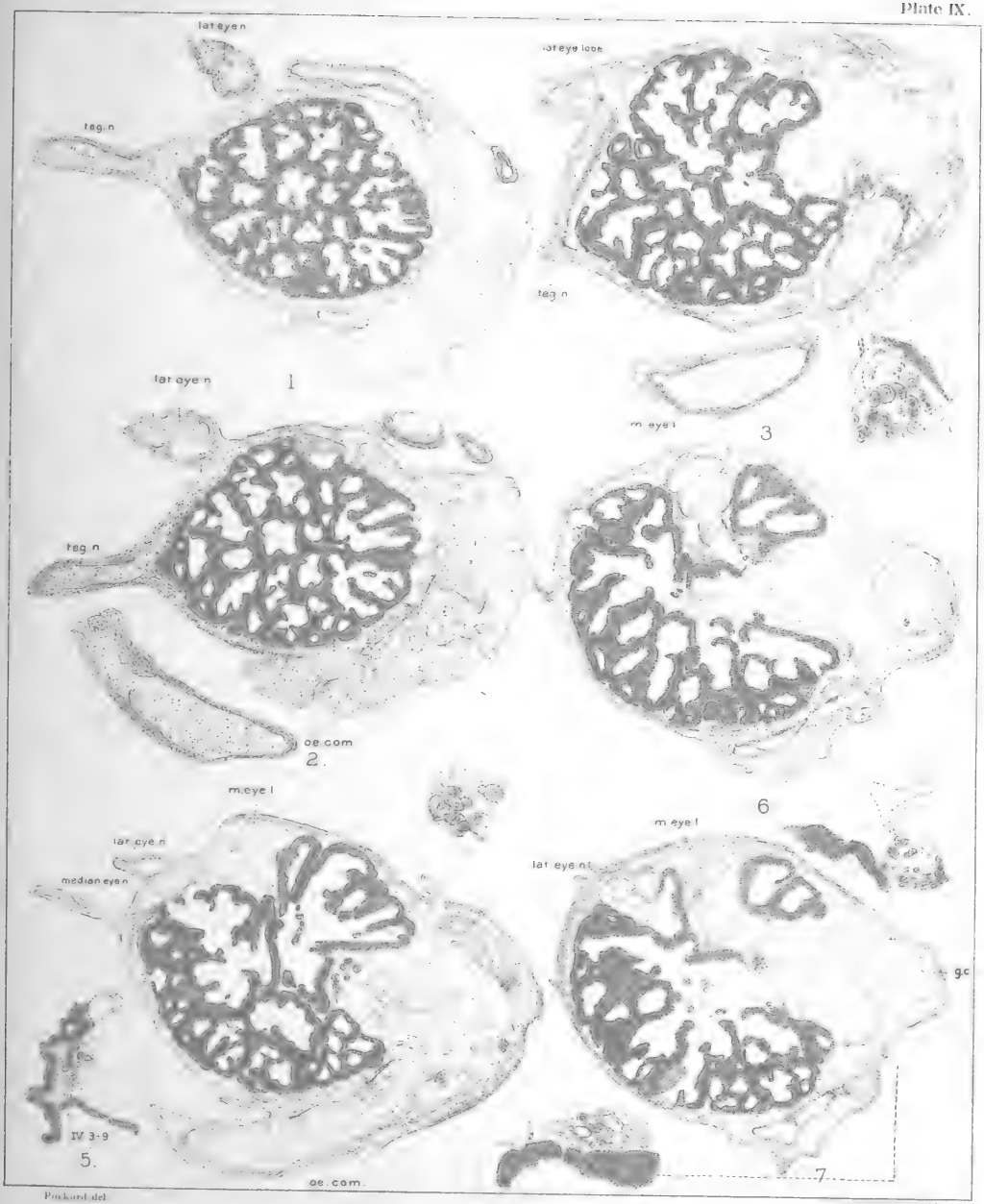
Horizontal Section through the brain of a young Limulus.

Horizontal Sections through the brain of a young Limulus.



Horizontal and sagittal Sections through the brain of a young Limulus.



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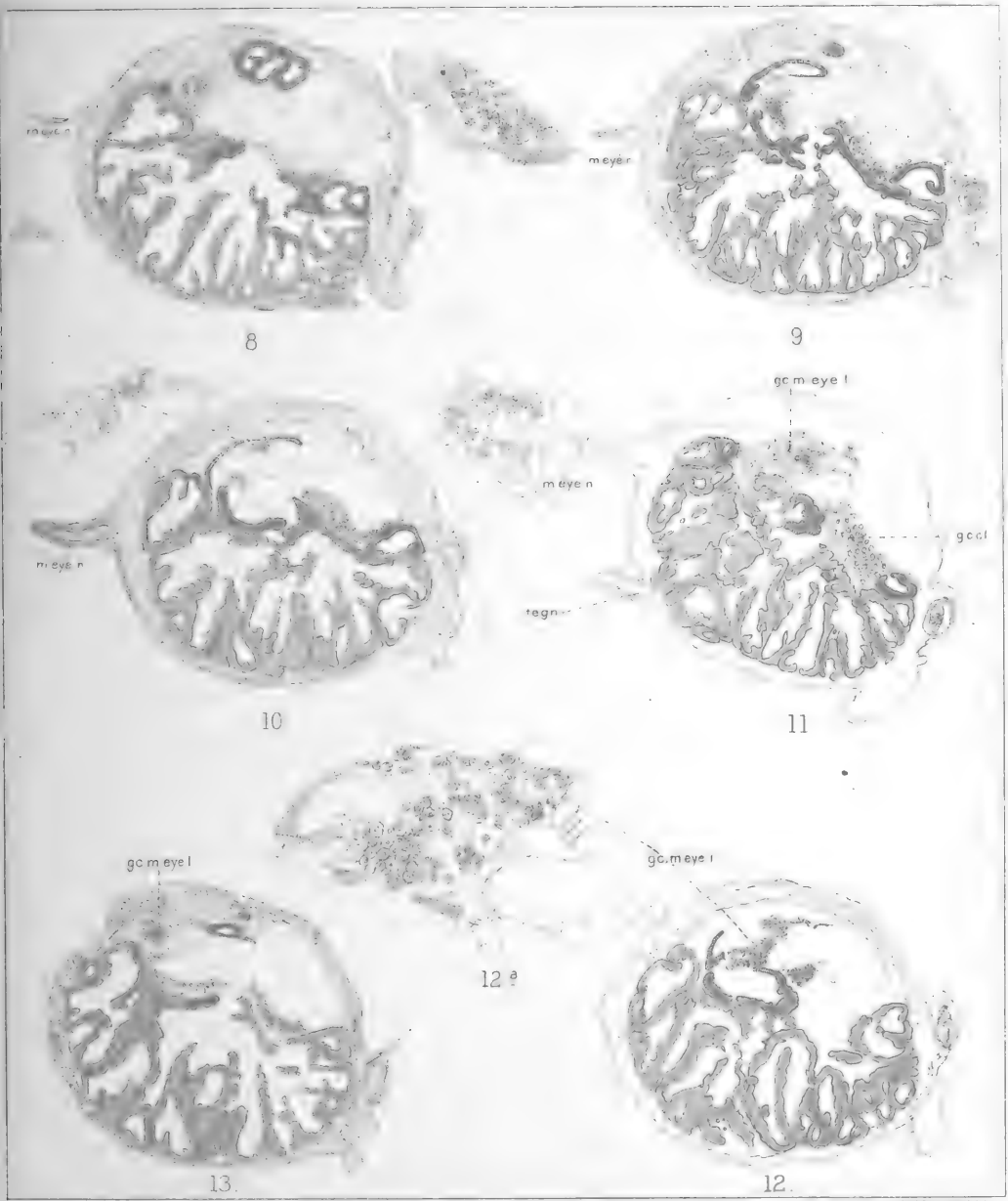
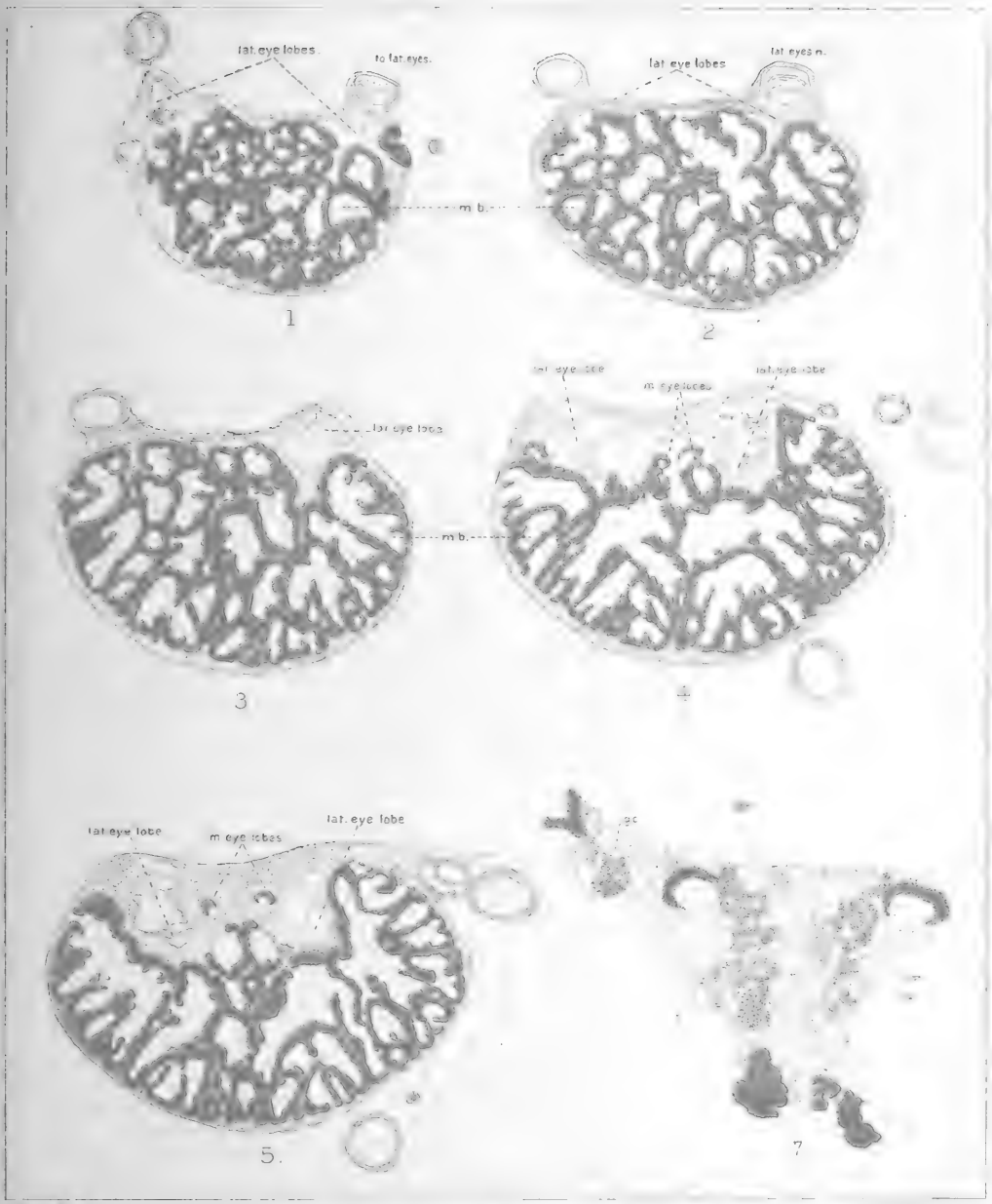
Longitudinal sections of the brain of Limulus.



Longitudinal (sagittal) Sections of the brain of Limulus.



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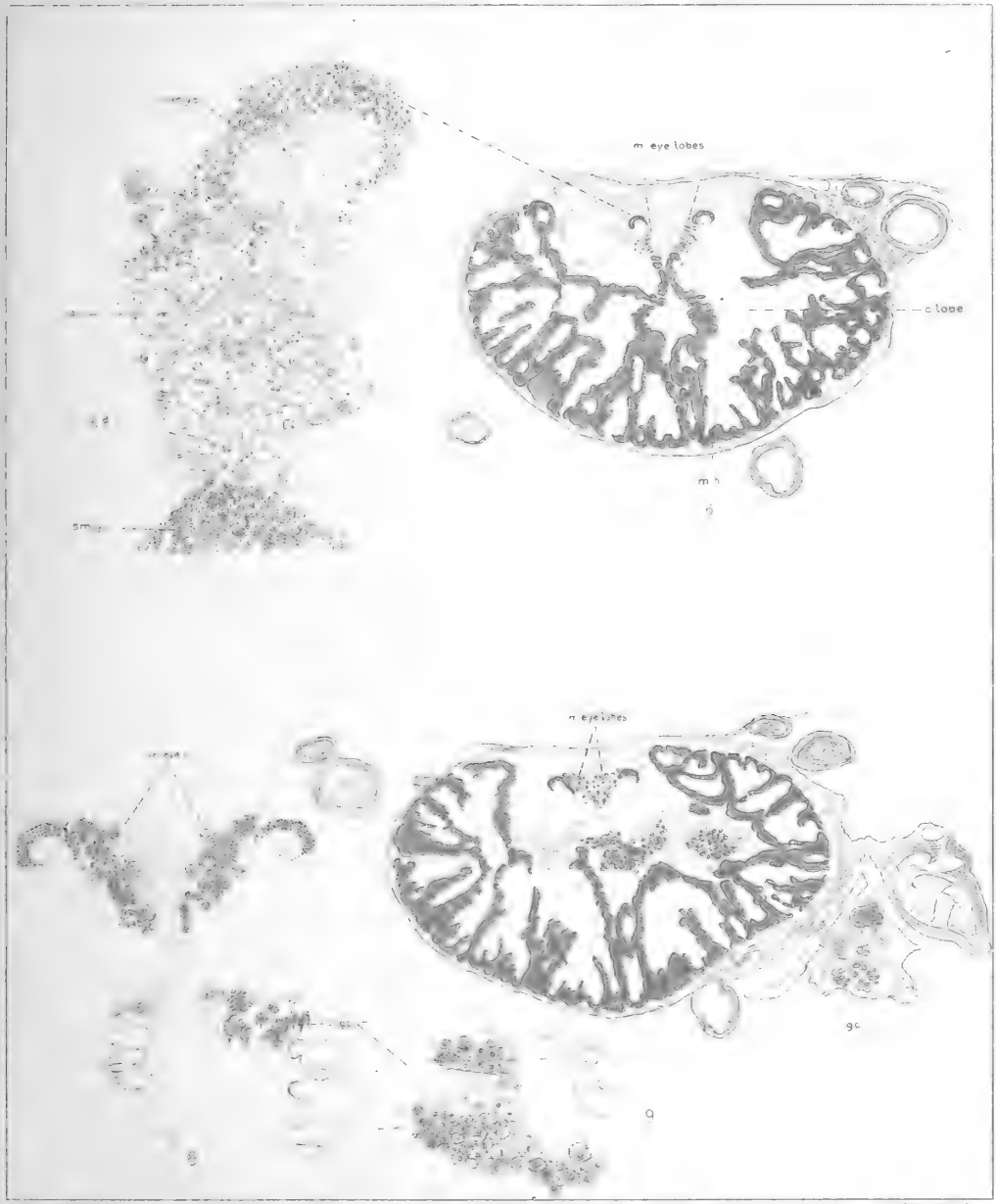
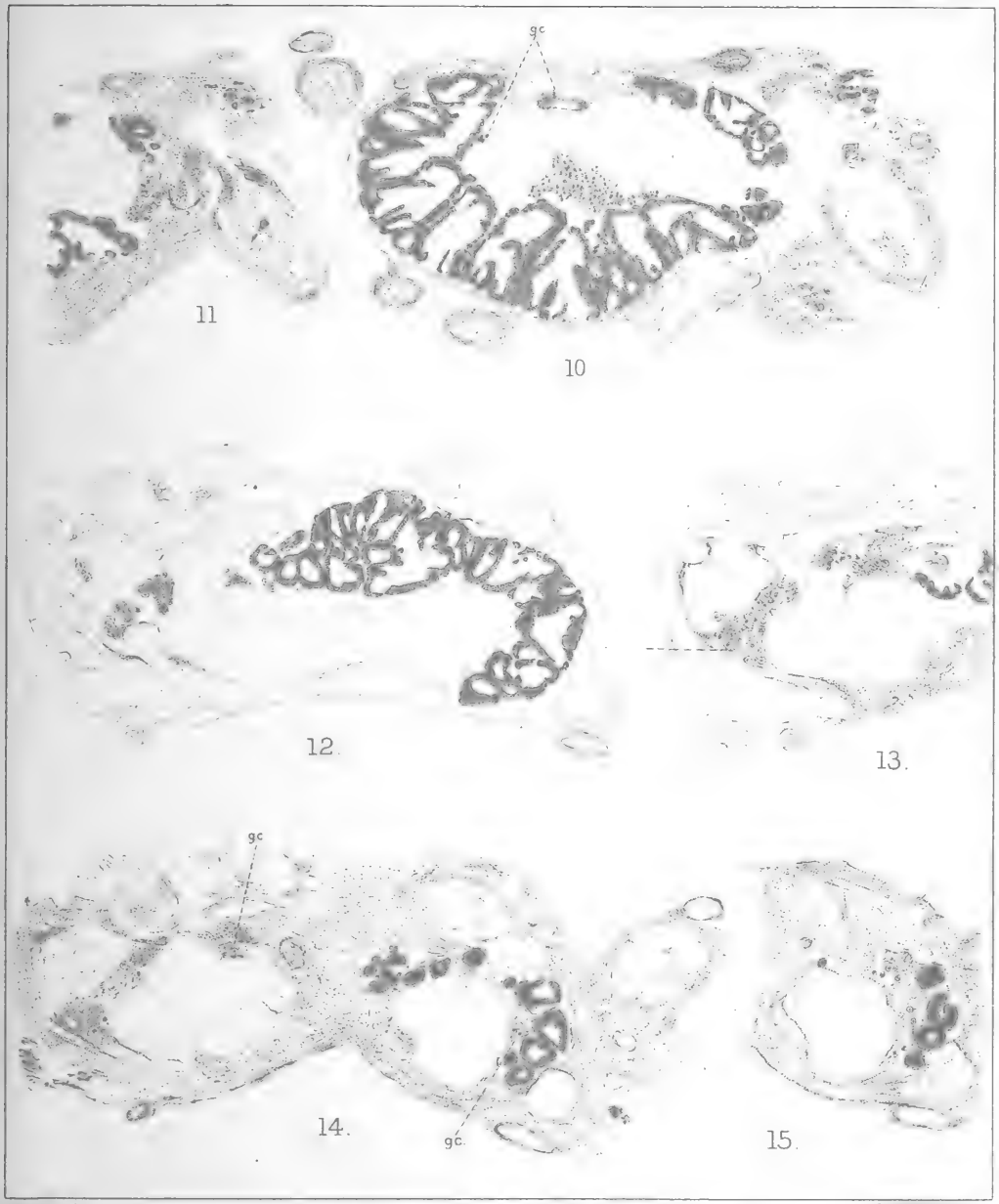
Transverse Sections of the brain of Limulus.



Transverse sections of the brain of Limulus.



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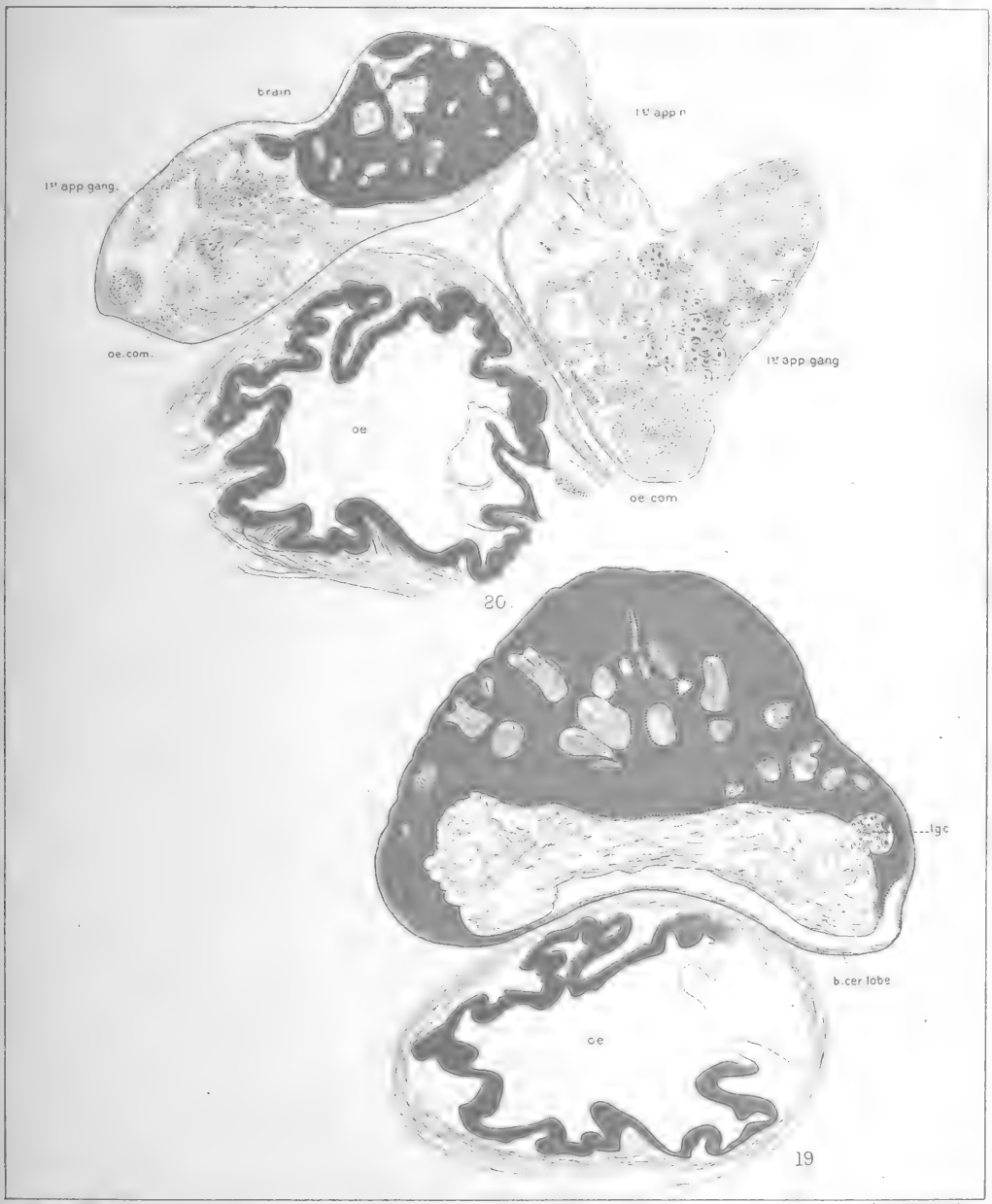
Transverse Sections through the brain of Limulus.

Transverse Sections through the brain of Limulus.



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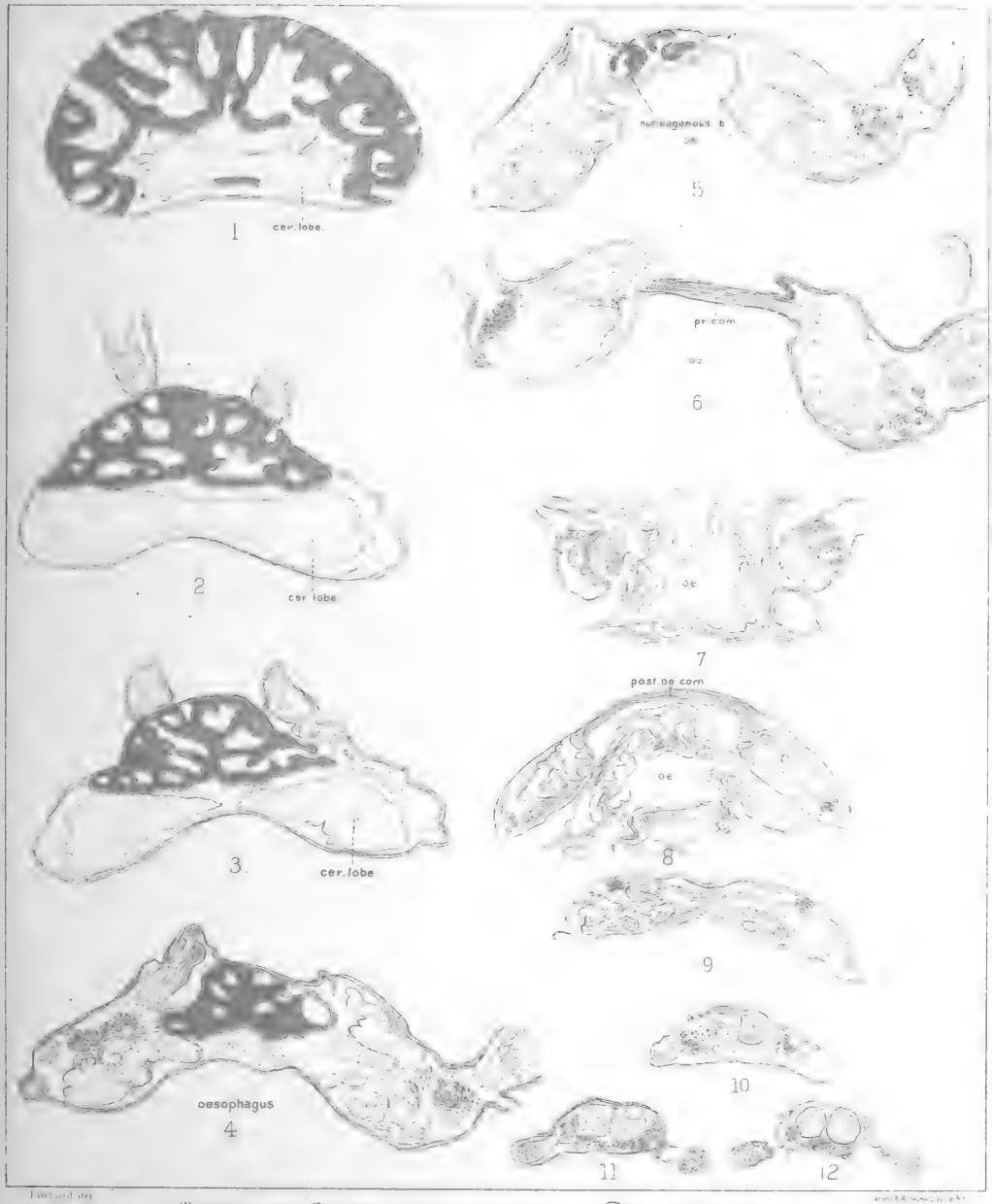
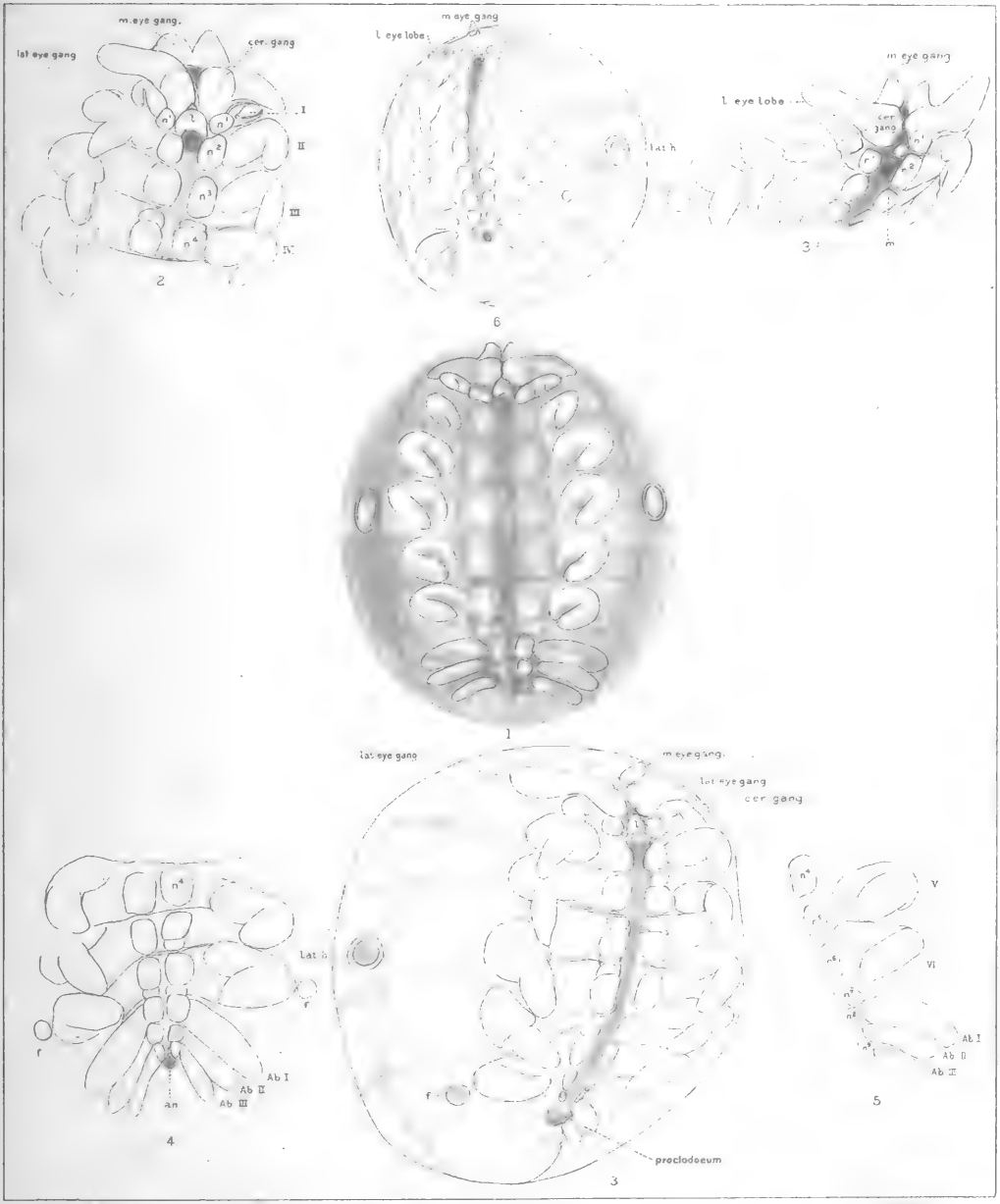
Transverse sections through the brain of Limulus.



Transverse Sections through brain and oesophage at ring



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Embryo of Limulus showing the primitive optic and cerebral ganglia.

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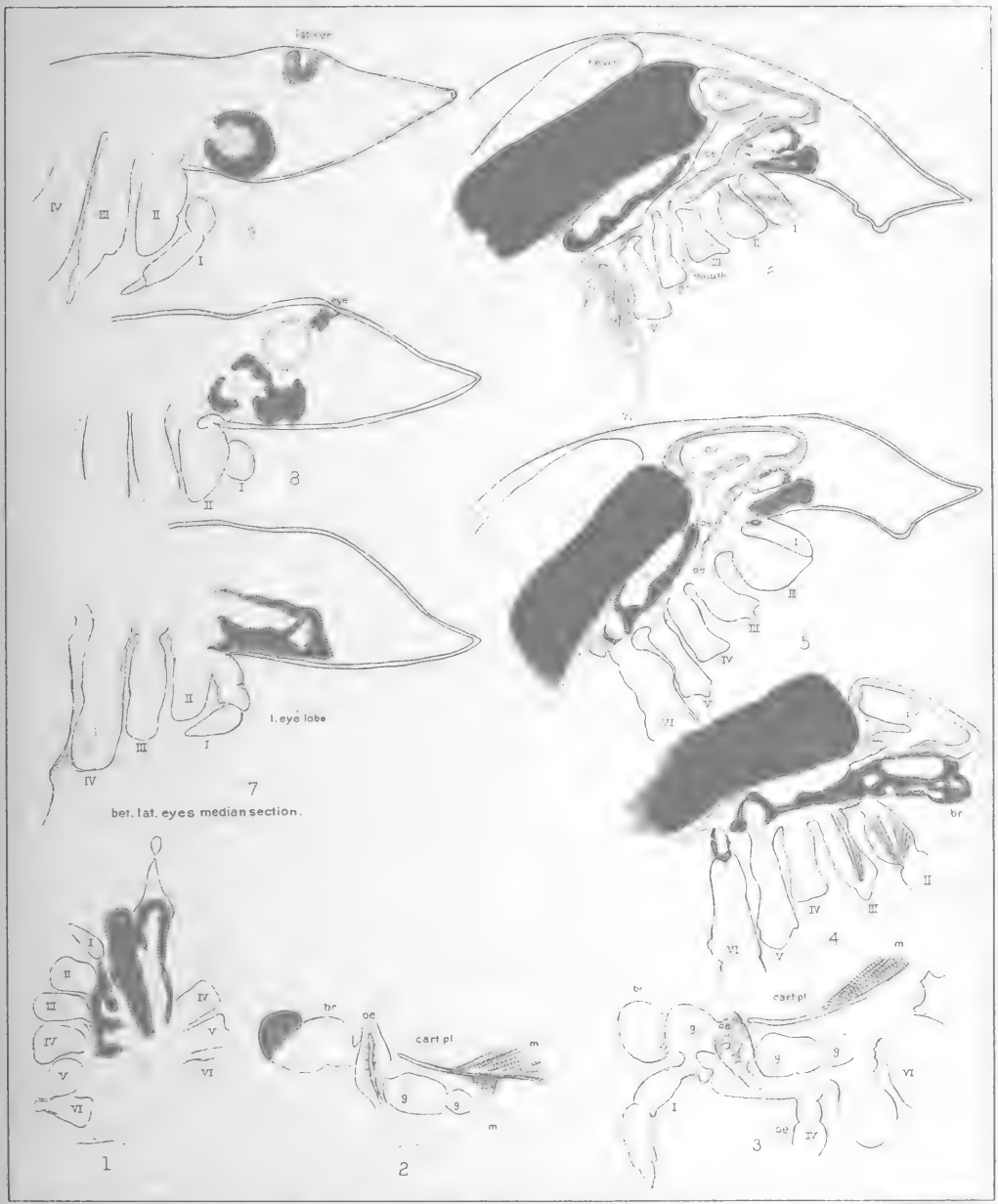

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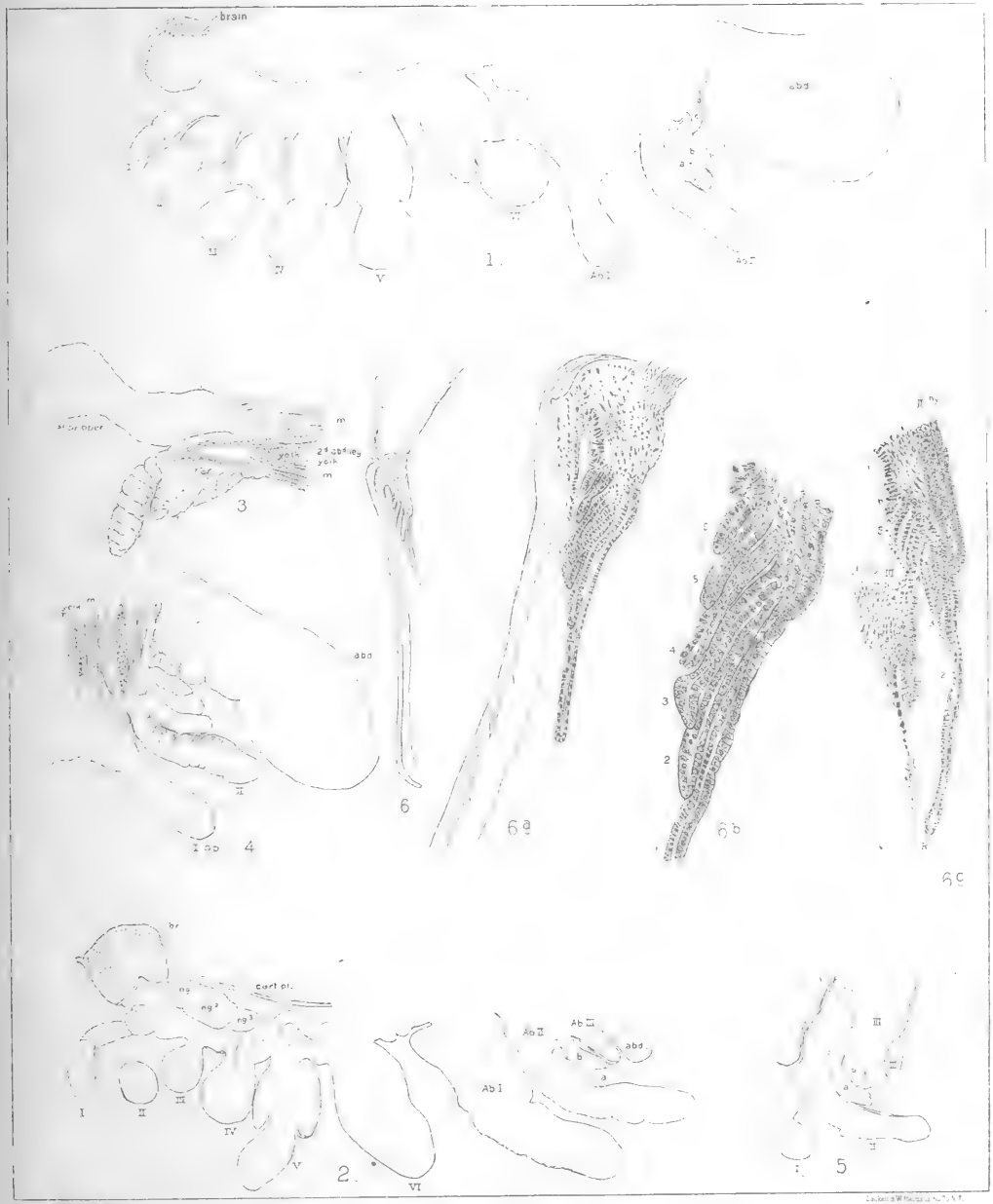
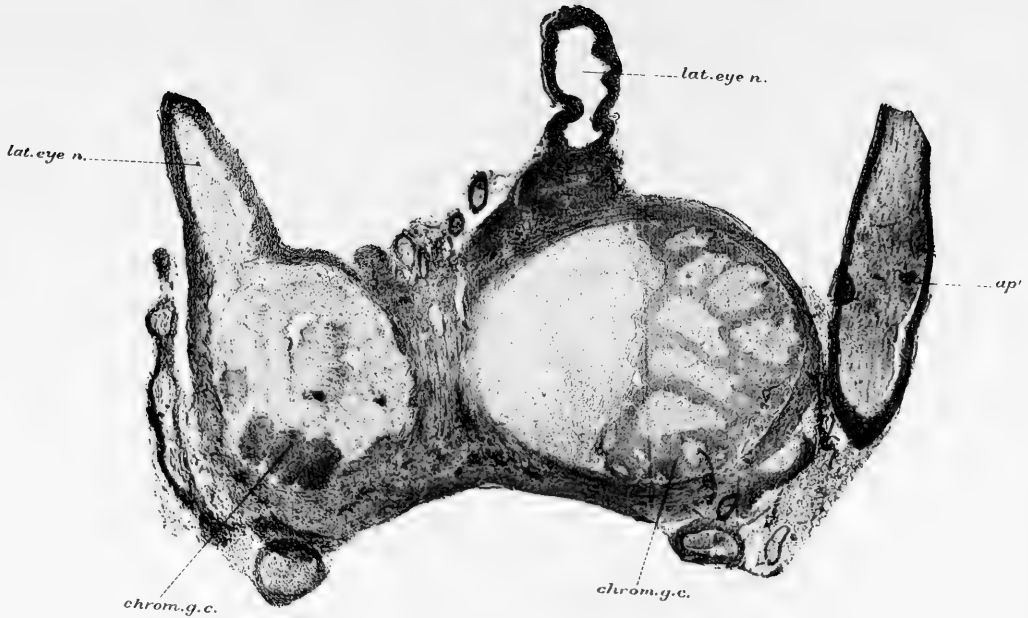
Sections of the brain, etc. of the larval Limulus.



Development of the abdominal legs and the gills.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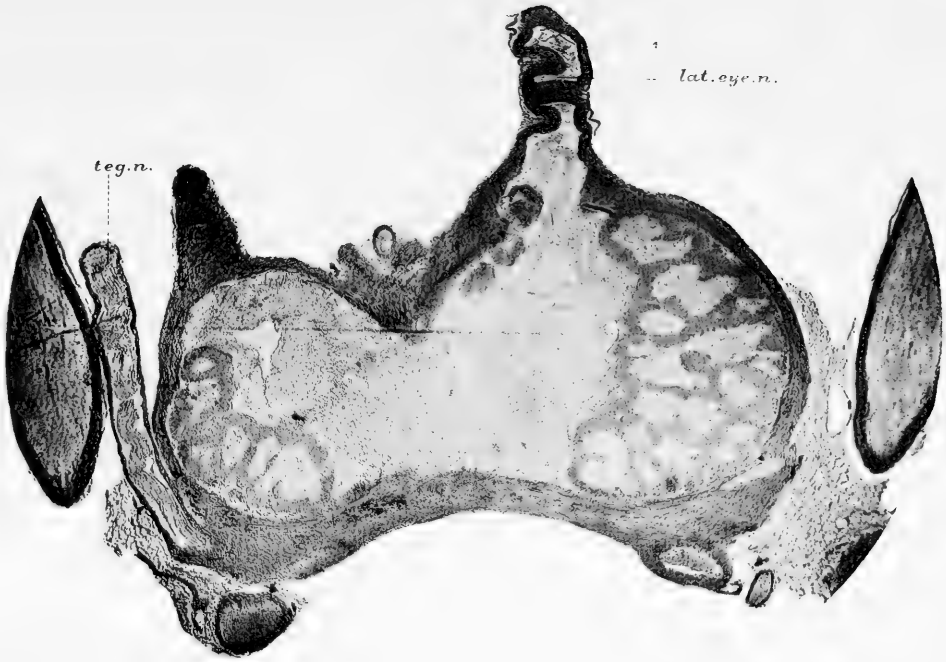
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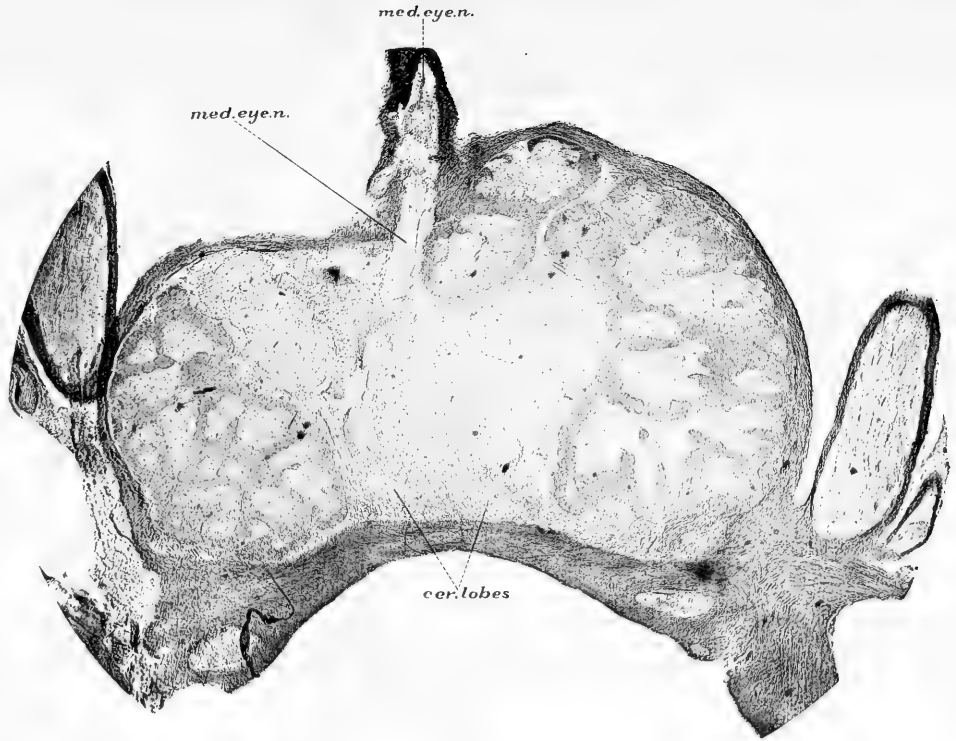
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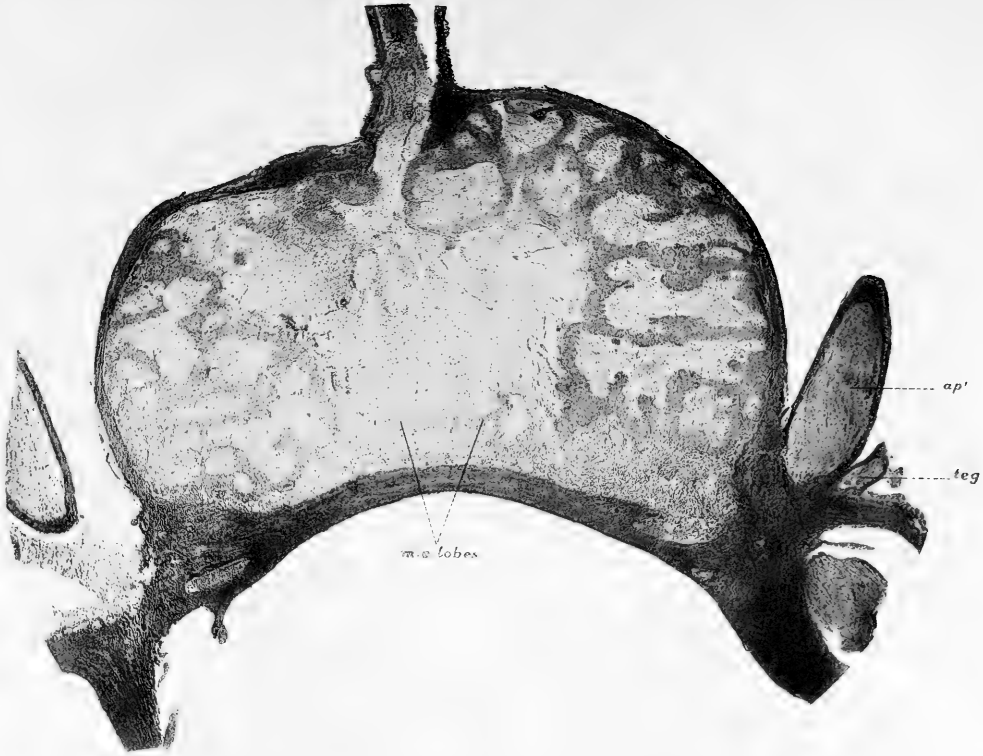
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PLATE XXVI.

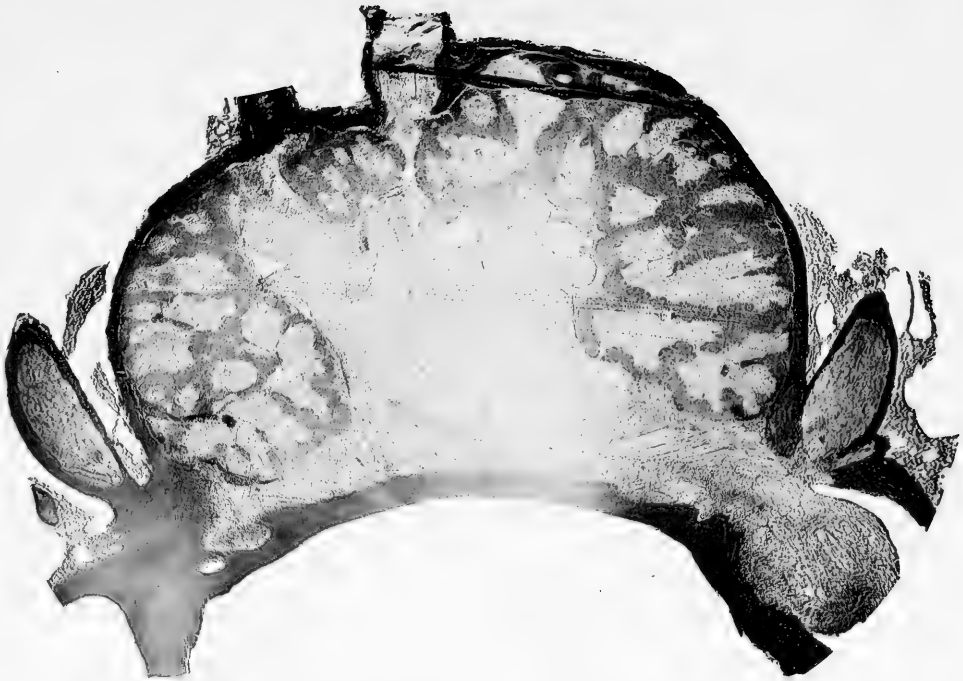

PLATE XXIX.

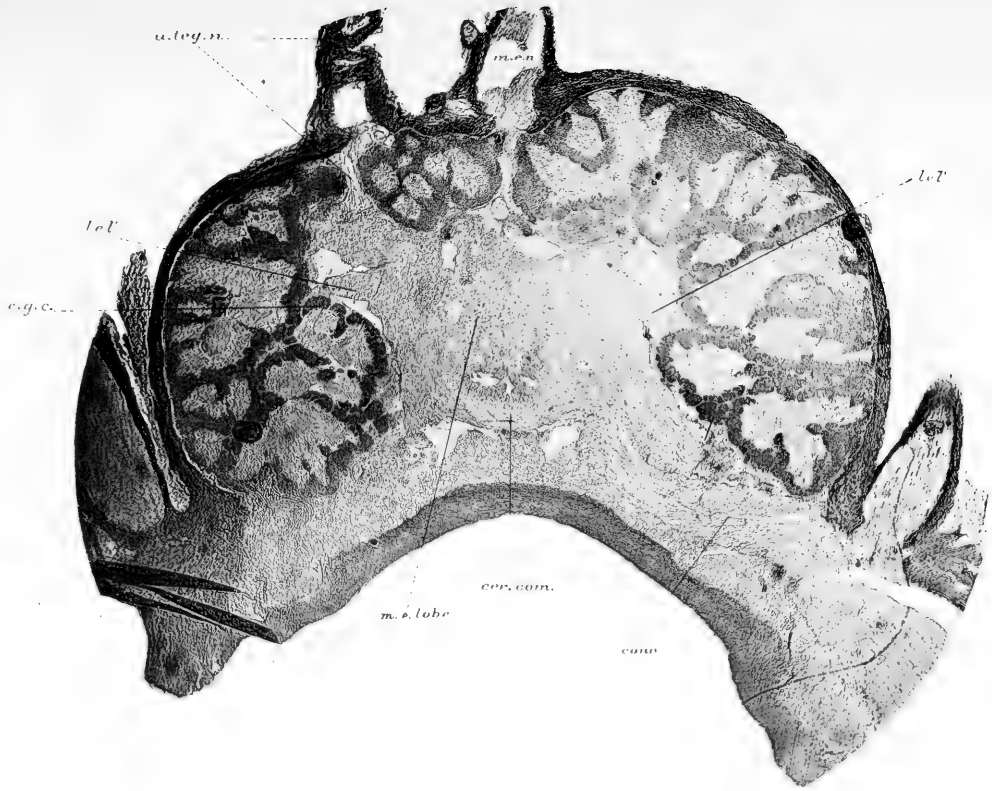

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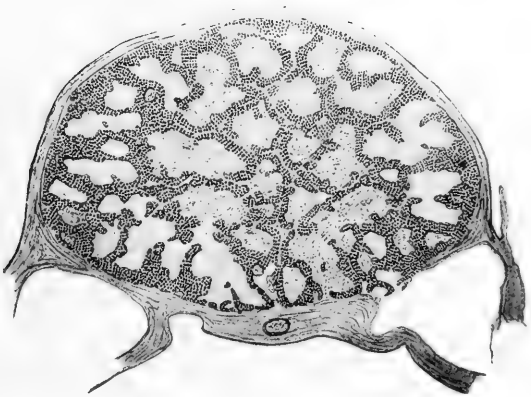
PLATE XXXI.



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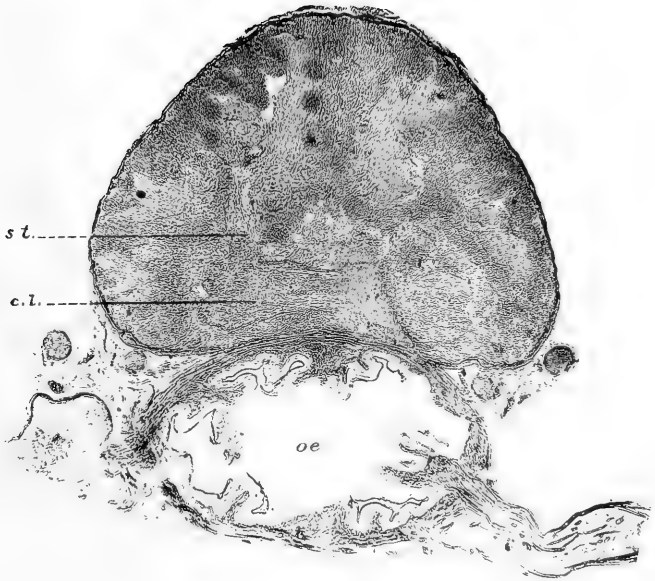

PLATE XXXIII.

PLATE XXXIV.

PLATE XXXV.

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